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July, 1906

Editors: JOHN M. COULTER and CHARLES R. BARNES

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EDITORS:

JOHN MERLE COULTER AND CHARLES REID BARNES

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ERRATA

Vol. 41: p. 394, legend, for *fig. 3*, read *fig. 4*.
P. 16, line 17, for 15^{cm} read 25^{cm}.
P. 17, line 1, for 15^{cm} read 25^{cm}.
P. 21, line 3, for 1889^{m} read 2000^{m}.
P. 32, line 11, for (*fig. 6*) read (*fig. 7*).
P. 66, line 20, for WEIS MAN read WEISMANN.
P. 141, line 15, add Nov. 15.
P. 164, line 11 from bottom, for concluding read including.
P. 165, line 10, for dioecious read monoecious.
P. 308, line 10, for some read deeper colonies.
P. 308, line 20, for boullion read bouillon.
P. 312, line 15, for ROBERTSON read ROBINSON.

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BOTANICAL GAZETTE

JULY, 1906

ON CRETACEOUS PITYOXYLA.[1]

E. C. JEFFREY AND M. A. CHRYSLER.

(WITH PLATES I AND II)

In a recent publication Dr. Arthur Hollick[2] has described the discovery of amber in the Raritan formation of the Middle Cretaceous, at Kreischerville, Staten Island. The amber in question occurs in largest quantity "in a stratum or bed, characterized by layers and closely packed masses of vegetable débris, consisting of leaves, twigs, and fragments of lignite and charred wood." Lignite occurring in association with amber at Cape Sable, Magothy River, Anne Arundel County, Maryland, collected by Professor A. Bibbins of the Woman's College, Baltimore, and of somewhat similar geological horizon, has recently been determined by Dr. F. H. Knowlton[3] of the United States Geological Survey as a new species of Cupressinoxylon. It appeared desirable to one of us that the lignites associated with the Kreischerville deposits of amber should be subjected to microscopic examination, in view of the possibility that the succiniferous ones might also turn out to belong to an extinct species of Sequoia (Cupressinoxylon). On communicating with Dr. Hollick in regard to this possibility, he very kindly consented to a combined visit to the beds at Kreischerville, for the purpose of securing authentic specimens of the succiniferous and other lignites. On April 18, 1905, we examined together the various

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[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 5.

[2] Amer. Nat. **39**:137–145. 1905. Contributions from the New York Botanical Garden, No. 64.

[3] American amber-producing tree. Science N. S. **3**:582–584. *figs. 1–4.* 1896.

excavations in the Cretaceous clays at Kreischerville, particularly that known as the Androvette pit, where the largest quantities of amber have been found. We were fortunate enough on this occasion to secure a large quantity of lignites, including several fragments of some size, showing the amber *in situ.* On a subsequent visit, in the following autumn a further supply of material was secured, including some admirably preserved Pityoxylon from a newly opened excavation known as the Drummond pit.

The lignites gathered at Kreischerville belong to at least three genera: Araucarioxylon, Cupressinoxylon, and Pityoxylon. Of these only the last proved to be succiniferous. The first two genera mentioned represent several species and present features of very considerable interest, but it is not our intention to discuss them further here. The pityoxyloid lignite containing masses of amber was found in the form of large pieces from the various excavations at Kreischerville, as well as in smaller fragments occurring in the amber-bearing strata themselves, at the Androvette pit, as described by Dr. HOLLICK (*l. c.*). The amber enclosed in lignite appears both in the translucent shining condition and in the dull ochraceous modification. In the latter state it is particularly conspicuous on account of the contrast in color with the black lignite, and may be made out not only in the form of pockets and nuggets, but also as fine yellow threads or streaks corresponding to the normal resin passages of the wood. Unfortunately the state of preservation of most of the succiniferous lignites left something to be desired. In the Drummond and Androvette pits, however, were found a number of partially charred, and, as a consequence, exquisitely preserved Pityoxyla, which were apparently specifically identical with or at any rate closely allied to the actually succiniferous fragments of Pityoxylon. It has been thought advisable to defer the description of the amber-containing lignites until a greater quantity of material should be accumulated, which might not only be better preserved, but might also throw some light on the conditions leading to the formation of amber. The partially charred lignites belonging to the genus *Pityoxylon* Kraus appear, nevertheless, worthy of immediate investigation, both because they show features of considerable phylogenetic interest, and because the genus Pityoxylon is considered by some paleobotanists not to antedate the Tertiary.[4]

The specimens of Pityoxylon, which have served as the material for the present investigation, consist for the most part of cylindrical fragments, which are sometimes as thick as 10^{cm} and often twice as long. Most of them however are of smaller size. Where the pieces are cylindrical they generally include the pith in a good state of preservation, a feature of some importance in connection with their diagnosis. It is not possible to state absolutely from the nature of the specimens whether they represent smaller branches or merely the core of larger axes from which the external layers have been burned off. From the ordinarily tylosed condition of the resin canals, it may be inferred with a strong degree of probability that the latter supposition is more likely to be correct. Angular fragments showing annual rings with a large radius of curvature permit a study of the structure of the older wood. Although at least two different species of fascicles of pine needles and at least as many species of cone scales of Pinus, all in an admirable condition of preservation, have been found in association with the Pityoxyla from the Androvette pit, it has not been possible to distinguish in these lignites more than one type of wood structure. The material in this respect presents an interesting parallel to the condition found by CONWENTZ[5] to exist in the Pityoxyla of the Eocene or early Oligocene, which bear the well-known Baltic amber; for this author declares that he is unable in the vast variety of fossil succiniferous woods which have passed under his inspection to diagnose more than a single species. The absence of clearly marked criteria for the separation of species on the basis of wood structure is not surprising, since even in the case of living pines it is difficult to do more than segregate the various species into larger groups or sections on the characters offered by the wood.

Fig. 1 shows the structural features of a transverse section of a slightly flattened branch about 5^{cm} in thickness in its greatest diameter, and showing more or less distinctly about twenty annual

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[4] *Cf.* GOTHAN, Zur Anatomie lebender u. fossiler Gymnospermen-Hölzer 88. Herausgeb. von der Königlich Preussischen Geologischen Landesanstalt und Bergakademie. pp. 108. Berlin, 1905.

[5] Monographie der Baltischen Bernsteinbäume. Danzig, 1890.

rings. It is to be observed from the photograph that the annual rings are not as strongly marked as they are in pines of the present day. This feature is due to the less pronounced thickening of the tracheids of the summer wood. There are no parenchyma cells present in the wood except those which surround the resin canals. The rays are strongly marked on account of the resinous character of their contents, a feature of difference from modern pines, where as a rule the ray-cells are quite free from the dark brown secretion which is characteristic of the resiniferous cells in the Cupressineae and in the genera Cedrus and Tsuga among the Abietineae. The resin canals show a tendency to become aggregated in clusters. They may be almost absent in one or more annual rings and correspondingly abundant in others. The resin ducts are surrounded by highly resiniferous cells and appear not to be confined to any special region of the annual ring. On the left of the figure is to be seen a resin canal occluded by tyloses.

Fig. 2 shows a section of the same branch which includes a portion of the pith. The medullary cells are filled with dark brown contents. Sclerified cells are quite absent in the pith. To the right of the photograph a process passes off from the medulla, which is the pith of a small branch, in all probability a brachyblast or short shoot. In the wood immediately adjoining the pith may be seen a number of resin canals, closely filled with tyloses. The position of these resin canals in relation to the pith is that found among living species of Pinus, in the hard pines (*Scleropitys* auct.), in which the resin canals also abut on the pith, in some cases actually occurring in the primary wood, in contrast to the soft pines (*Malacopitys* auct.), where the resin ducts are somewhat remote from the pith and never occur in the primary wood. The annual rings are generally less well marked in proximity to the medulla than in the more external part of the wood.

Fig. 3 is a longitudinal radial view of the wood of the same specimen illustrated in the two preceding photographs. The section shows a single vertical and several anastomosing horizontal resin canals, all quite filled with tyloses. A careful inspection indicates that the wood is made up of tracheids, which are provided with a single vertical row of radial bordered pits.

Fig. 4 shows the structure of the wood in the same specimen, as seen in tangential section under a low magnification. The rays are of the two kinds found in *Pityoxylon* Kraus, namely, linear and fusiform.

Fig. 5 shows a tangential view of part of the same section, more highly magnified. In this view the radial pits of the tracheids may be seen in profile, and on the left a face view of a few tangential pits. In some of the rays dark contents may be made out in the cells, which have partially shrunk away from walls. This is apparently of the same nature as the dark brown material found in the resin cells of certain living conifers. The interesting fact to be noted is that the resin occurs equally in the marginal and in the central cells of the ray. This feature may be clearly distinguished in two of the rays on the lower left portion of the photograph. In living pines resin never occurs in the marginal cells of the ray, which, as is well known, are not true parenchymatous cells, but are of a tracheary nature. They are in fact variously described as marginal tracheids, horizontal tracheids, and tracheidal cells.

Fig. 6 shows another portion of the same section as that represented in *fig. 4*, on the same scale of magnification as *fig. 5*. This figure shows very clearly the occurrence of tangential pits, which are confined to the autumnal tracheids as in certain living species of Pinus. In *figs. 5* and *6* may be seen fusiform rays containing horizontal resin canals occluded by tyloses.

Fig. 7 represents a transverse section, under high power of magnification, of the autumnal wood of a specimen showing annual rings with a large radius of curvature. The elements are much larger in this instance, as is the rule in the older wood of the Coniferales in general. The tangential pits of the autumnal wood can be very clearly made out. We have found no specimen of Pityoxylon from the Kreischerville deposits in which the tangential pitting of the autumnal tracheids is not a marked feature. CONWENTZ has pointed out that this feature is also present in the autumnal wood of the Baltic amber-producing trees (*l. c.*, p. 21).

It will be inferred from the above description that the Cretaceous Pityoxyla just described differ in several features from the woods of any modern or even Tertiary species of Pinus. The leafy short-shoots found in intimate association with the Pityoxylon here described, which unquestionably belong to the genus Pinus in the narrower sense, have the double bundle which is characteristic of the hard pines,[6] as has been learned by one of us from a microscopic investigation of their structure. They are also provided with the persistent foliar sheaths, which are a striking feature of the hard or pitch pines in contrast to the soft pines, which have deciduous sheaths. All the numerous cone scales found in intimate association with the wood, illustrated in our *figs. 1–7*, are equally characteristic of the hard pines, for they have the thickened apophysis and median umbo, which are unfailing features of that group. In the case of our Pityoxylon, however, we find universally present the tangential pits of the autumnal tracheids, which are characteristic of the existing soft pines.[7] STRASBURGER, however, states that he has found tangential pits to be present in the autumnal wood of *Pinus canariensis* and *Pinus rigida*. MAYR[8] has also called attention to the occasional occurrence of tangential pits in the autumnal wood of one group of the hard pines. This feature has also not escaped the notice of CONWENTZ. One of us has observed the very frequent occurrence of tangential pits in the autumnal wood of the *cone* in various species of hard pines, where they are quite absent in the vegetative wood. This is the case, for example, in the woody axis of the cone of *P. Pinaster*, the vegetative wood of which is described by KRAUS[9] as having no tangential pits. *P. palustris* too, although it is a characteristic hard pine, in the absence of tangential pits from its autumnal wood,[10] possesses these in great abundance in the autumnal wood of its cone, in both the annual rings present. These two examples will suffice to illustrate the fact that tangential autumnal pits, such as are ordinarily absent in the wood of hard pines, are generally present in their *cones*. It may be inferred from the mode of their occurrence that tangential

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[6] COULTER and ROSE, Synopsis of North American pines based on leaf-anatomy. BOT. GAZETTE 11:256, 302. 1886.

[7] PENHALLOW, Anatomy of the Coniferales. Amer. Nat. **38**:243. 1904. STRASBURGER, Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen.

[8] Waldungen Nordamerikas.

[9] Beiträge zur Kenntniss fossiler Hölzer, p. 25.

[10] PENHALLOW, *loc. cit.*, :04.

bordered pits in the tracheids of the hard pines are an ancestral feature. It is accordingly not surprising to find them more commonly present in older types of hard pines than those now living. Conwentz in his admirably accurate and thorough account of the wood of *Pinus succinifera* notes their invariable presence in this species, which on account of its denticulate marginal ray-tracheids must be considered to belong to the hard pines. As has already been pointed out, the structure of the associated leaf fascicles and cone scales leads to the conclusion that the Cretaceous Pityoxylon under discussion belongs also to a hard pine. The mode of occurrence of the resin canals in the medullary crown, which is illustrated in *fig. 2*, is also that which is characteristic of the hard pines.

The most reliable feature of difference separating histologically the hard pines from the soft pines is the occurrence of denticulate marginal tracheids in the former group. In the soft pines the marginal tracheids are entirely without denticulations. In our Pityoxylon, as has been shown above, marginal tracheids of any kind are quite absent; so that it is not possible on this feature to diagnose the affinity of our material with either of the two main groups of pines still living. It is of interest to note that the Cretaceous Pityoxylon under discussion has the general structure of the rays found in Abies or Pseudolarix, with the wood structure found in Tertiary and modern species of Pinus. There can be little doubt that in the peculiar structure of the rays we have to do with an ancestral feature; for if we take for example a modern species of Pinus, in which the marginal tracheids are well developed even in the first annual ring, such as *P. palustris*, we find the marginal tracheary cells entirely absent in most of the rays of the two annual rings of the female cone. It is well known that in many of the modern species of Pinus the marginal tracheary ray-cells do not appear until the branch is from one to several years old. The same feature, if one may judge from Conwentz' description, was also present to an even more marked degree in the Baltic amber pines, which are considered by Conwentz to belong to the early Oligocene or late Eocene. Another feature of striking resemblance presented by the wood of the *cones* only of existing species of Pinus, to the vegetative woods of Cretaceous Pityoxyla which we have investigated, is the highly resinous character of the ray-cells. This feature may also be well seen in *P. palustris*, already referred to. The contrast in the contents of the ray-cells as they occur in the wood of the cone or of a vegetative branch is very strongly marked.

It may be inferred that we have overlooked the presence of tracheary marginal cells in the Cretaceous Pityoxyla, which are the subject of the present article. This view cannot however be accepted, as the wood of some of our partially charred specimens is in a perfect condition of preservation, often not even showing the spiral striations which are generally found as a feature of decay in many fossil woods, otherwise well preserved. Moreover, in shallow rays consisting of a single stratum of cells, which in the case of modern species of Pinus are composed entirely of tracheids, the cells are parenchymatous and invariably filled with a dark brown resinous content, which leaves no doubt as to their histological nature. The cells on the margins of the rays in our Pityoxylon are moreover related to the central cells of the rays and to each other by simple pits and not by bordered pits, as is the case with the marginal tracheids. It is obvious that the ray-structure of Pinus underwent a great change in the passage from the Mesozoic to the Tertiary period.

On account of the geographical occurrence of the Pityoxylon, which has just been described, it is called **Pityoxylon statenense.** The diagnosis is as follows:

Transverse.—Annual rings narrow, sometimes not clearly marked; wood parenchyma absent except in the periphery of the resin canals, which may occur in any part of the annual rings and are often stopped with tyloses; rays highly resinous; bordered pits present on the tangential walls of the autumnal tracheids; tracheids about 25 μ in diameter.

Radial.—Radial pits of tracheids about 17 μ in diameter, in a single vertical row, round with a round mouth; pits of the ray-cells about one per tracheid, round or somewhat elliptical, 10 μ in diameter; ray-cells all parenchymatous, very resinous, length from 100 to 120 μ; marginal ray tracheids quite absent.

Tangential.—Rays of two kinds, linear and fusiform, the latter containing resin canals which are surrounded with rather thick-walled parenchyma; resin canals often occluded by tyloses; tangential pits present in the autumn wood.

In addition to the Pityoxylon described above, we have examined another of the same type, which was secured by Dr. ISAAC BOWMAN from a newly exposed section at Third Cliff, Scituate, Mass. Although there is some question as to the exact geological age of the strata from which it was taken, it is considered desirable to refer to it at the present time on account of the interesting similarity to the species discussed above. DR. BOWMAN describes[11] the section from which the material was taken as follows: "The section at Third Cliff shows yellow clays at the base conformably overlain by yellow and white sands and succeeded by a bed of bright red sands with an unconformity at their base. On the eroded edges of the red and white beds are deposited dark glauconitic and lignitic clays and sands. The entire series of beds has a total maximum thickness of 60 or 70 feet and outcrops for half a mile along the cliff face. Absolutely no erratic material occurs either within the beds themselves or along the lines of unconformity." The lignite to be described came from the "lignitic sands and clays" just mentioned.

The material consisted originally of several laminated and badly preserved fragments, together with one larger piece, cubical and about 12^{cm} in its three dimensions. The better-preserved fragment has served as the basis of the following description. As the result of decay and pressure, the lignite has suffered some compression both in the radial and tangential planes. The stress in the radial plane has produced a considerable sinuosity in the course of the wood rays. The annual rings cannot be made out with the naked eye or even with a pocket lens of some degree of magnification.

Fig. 8 shows a magnified portion of a transverse section of this wood. The area of the photograph includes parts of two annual rings. The line of demarcation is very indistinct and runs obliquely a little above the lower third of the photograph. The rays are very dark on account of the highly resinous character of their contents. Two large patches of parenchyma may be seen surrounding two vertical resin canals. The large amount of resiniferous parenchyma about the canals is particularly characteristic of this species. There are no parenchyma cells in the wood other than those surrounding the resin canals. The annual rings have a very slight radius of curvature and are somewhat distorted on account of the compression of the wood, although the elements which compose them are well

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[11] Science N. S. **22**:993–994. 1905.

preserved. The lignite under discussion obviously is part of an old stem.

Fig. 9 is a radial view of the wood of the Pityoxylon from the cliffs at Scituate. This view shows the extremely resinous character of the rays, which doubtless is largely responsible for the good preservation of the wood, as, unlike the material of *Pityoxylon statenense,* it has not been charred in any way by fire. The rays are quite without tracheidal marginal cells and in this respect resemble those of the first described species, and differ from the ray vegetative structure found in any modern species of Pinus.

Fig. 10 shows a tangential view of the wood. The rays are obviously of two kinds, namely, linear and fusiform. The former are often very deep, and in this feature present a marked contrast to the first described species of Pityoxylon. The fusiform rays are usually occupied by a horizontal resin canal, the lumen of which is often filled with a dark brown material similar to that found in the surrounding resiniferous cells of the ray. Tyloses have not been found either in the horizontal or the vertical resin canals of this species.

Fig. 11 shows a portion of the same section more highly magnified. The highly resinous character of the rays can clearly be made out. There is one fusiform ray present containing a horizontal resin canal, which is filled with a dark brown material similar to that found in the ray-cells. It may here be stated that in spite of the fact that the cells surrounding the lumina of the horizontal and vertical resin ducts cannot be described accurately as being thick-walled, nevertheless the ducts are never occupied by tyloses.

Fig. 12 shows another tangential view under considerable magnification. This illustrates the fact that in the rays the marginal as well as the central cells contain the same dark brown resin, as has already been referred to in the case of the other Cretaceous Pityoxylon described above. The wood is so well preserved that there can be no question as to the absence of marginal tracheids, such as occur in the rays of living species of Pinus and allied genera. Not only are the marginal cells filled with the same dark resinous material as the other cells of the ray, but they are related radially to each other, as well as to the central cells of the ray, above and below by simple pits.

This species of Pityoxylon is named **Pityoxylon scituatense,** from its place of origin. The diagnosis is as follows:

Transverse.—Annual rings moderately broad, indistinctly marked; resin ducts present, surrounded by a very deep zone of resiniferous parenchyma, without tyloses but sometimes filled with dark resinous contents; wood parenchyma quite absent; rays very dark and resinous; tracheids averaging 39 μ in diameter.

Radial.—Radial pits of the tracheids in a single row with the very oblique narrow mouths forming a cross, diameter of the pits about 20 μ; pits of the ray-cells generally one per tracheid with narrow oblique mouth, about 10 μ in diameter; ray-cells all parenchymatous, average length 340 μ, very resinous; marginal ray-tracheids quite absent.

Tangential.—Rays of two kinds, linear and fusiform, the former often very deep; fusiform rays containing horizontal resin canals, which are always free from tyloses although somewhat thin-walled, both kinds of rays very resinous; tangential pits present in some of the tracheids.

In the two species of Pityoxylon described above, we have to do with woods which resemble those of the existing pines, but which nevertheless differ from them in important particulars. The marginal ray tracheids, which are not only characteristic of Pinus but of the allied genera Picea, Pseudotsuga, and Larix, are quite absent in our two species. The question arises whether it is proper to include them within the genus Pityoxylon, which has recently been stated not to antedate the Tertiary.[12] There is much to be said for such a course. In the case of our *Pityoxylon statenense* there can be no reasonable doubt that we have to do with the wood of a fossil species of Pinus, from the abundant occurrence in intimate association with the lignites of charred remains of cone scales and leaf fascicles of pines. Any doubt as to the identity of these scales and foliar shoots has been removed by a study of their microscopic structure, as well as their external features. Further, one of us has observed from the study of the *cones* of living pines that the features which are characteristic of our fossil woods are exactly those which are found to be distinctive of the wood structure of the cones of the living species of Pinus. There can be little doubt that in the case of the wood of the cones of *Pinus palustris*, for example, the general absence of marginal tracheids, the highly resinous character of the rays, and the abundant presence of tan-

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[12] GOTHAN, *l. c.*, p. 88.

gential autumnal pits, all features of difference from the vegetative wood structure of existing hard pines, are ancestral characters, since such characters are wont to linger on in the reproductive axis. Indeed in no other way can the presence of these features in the wood of the cone be explained. It seems inadvisable to invent a new generic name for a fossil wood, which although lacking the marginal ray tracheids, which are characteristic not only of the wood of living pines, but of also Pityoxylon as generally defined, is beyond any reasonable doubt the wood of a Cretaceous pine. We find it difficult to follow GOTHAN (*l. c.*, p. 102) in establishing a new pityoxyloid genus of fossil woods, Pinuxylon, to which is assigned the ligneous characters of the living Pinus in the narrower sense. *Pityoxylon* Kraus seems rather in need of a wider than a narrower interpretation, if it is to include the wood of Pinus of the Cretaceous as well as Tertiary times. In the case of our *Pityoxylon statenense* there can be no reasonable doubt that we have to do with the wood of an extinct Cretaceous pine. It seems on account of its distinctive archaic features, however, inadvisable to name it under Pinus as CONWENTZ has rightly done in the case of the Tertiary *Pinus succinifera*, which is practically identical in its wood structure with modern hard pines. The retention of the genus *Pityoxylon* Kraus appears, for the present at any rate, absolutely essential in view of such cases as that presented by our *Pityoxylon statenense*. The evidence as to *Pityoxylon scituatense* is much less clear, as no cone scales or leaves have been found with it. Since, however, it presents the same general features as *P. statenense*, it may conveniently be included under the same genus.

There is good reason to believe from recent researches[13] that the genus Pinus in essentially its modern form, so far as the external features of the female cones go, existed as far back as the Jurassic. There is even evidence that the two great series of the hard and soft pines existed at this early period so that the geological extension of the genus must have been much more remote. Without considering the evidence for the existence of Abietineae at earlier geological periods than the Tertiary, furnished by impressions of the

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[13] FLICHE, P. et ZEILLER, R., Florule portlandienne des environs de Boulogne-sur-Mer. Bull. Soc. Géol. France IV. 4:787–812. 1904.

foliage, etc., there are now definite records, based on internal structure, which carry the group far into the past. KNOWLTON[14] has recently described an abietineous wood from the Jurassic beds of the Black Hills of Dakota which he calls *Pinoxylon dacotense.* It is characterized by the possession of vertical resin canals only, which are numerous and may occur in any part of the clearly marked annual rings. The structure of the tracheids and rays is that of the Abietineae. This author does not mention the presence of marginal ray tracheids, and in view of the fact that he describes the wood as admirably preserved, they probably may be considered to be absent here as in our Cretaceous Pityoxyla.

The *Pityoxylon Conwentzianum* of GOEPPERT from the Carboniferous of Waldenburg,[15] which has often been called in question, has received full confirmation from the description of a similar type of Pityoxylon, *P. chasense*, by PENHALLOW[16] from the Permian of Kansas. In these two species vertical resin canals are said to be absent, although the horizontal canals of the fusiform rays are clearly present. There is, accordingly, every reason to believe that the Abietineae are a very ancient group in their first appearance. In fact, they may be traced geologically quite as far back as the Araucarineae, which it is customary at the present time to regard as the oldest of the Coniferales. That they are not more numerously represented in the Mesozoic and earlier strata is probably entirely a matter of antisepsis, since araucarineous remains are in general much better preserved than are those of the Abietineae, where they are found imbedded together in the same strata. Mention need not be made here of the *Pityoxylon eggense* (Witham) Kraus and *Pityoxylon Hollicki* Knowlton,[17] since both of these appear to have been in a bad state of preservation.

The peculiar structure of the wood of Pinus in the Cretaceous, as distinguished from that found in the case of Tertiary and living pines, probably affords an explanation of the greater vigor of the

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[14] U. S. Geol. Surv. Ann. Rept. **20**^{2}: 420–422. 1898–1899.

[15] GOEPPERT, Revision meiner Arbeiten.

[16] North American species of Dadoxylon. Trans. Roy. Soc. Canada II. **6**^{4}: 76. 1900.

[17] Trans. N. Y. Acad. Sci. **16**: 134–136.

genus under modern conditions. It is generally inferred that genera which flourish under modern conditions cannot be of very ancient origin. This generalization, however, cannot be accepted in the case of Pinus, which, although found actually abundantly throughout the northern hemisphere in from 80 to 90 species, can be traced in obviously allied genera back to the Carboniferous. The appearance of marginal ray tracheids about the beginning of the Tertiary epoch, with the resulting improvement of water-supply, in all probability explains why so comparatively large-leaved a conifer should have been able not only to live on into the modern period, but to flourish as it never had before. Even at the comparatively early epoch of the Baltic amber beds (probably Eocene), there were numerous species present in the somewhat restricted area represented by that formation.

CONCLUSIONS.

1. The woods of certain pines of the Middle Cretaceous of Staten Island differed from those of existing pines (*a*) in the absence of marginal tracheids in the rays; (*b*) in the highly resinous nature of the rays; (*c*) in the association of characteristic features of the hard pines, as exemplified by leaf-fascicles, cone-scales, and structure of the primary wood, with the numerous tangential pits of the autumnal wood which are a feature of the living soft pines.

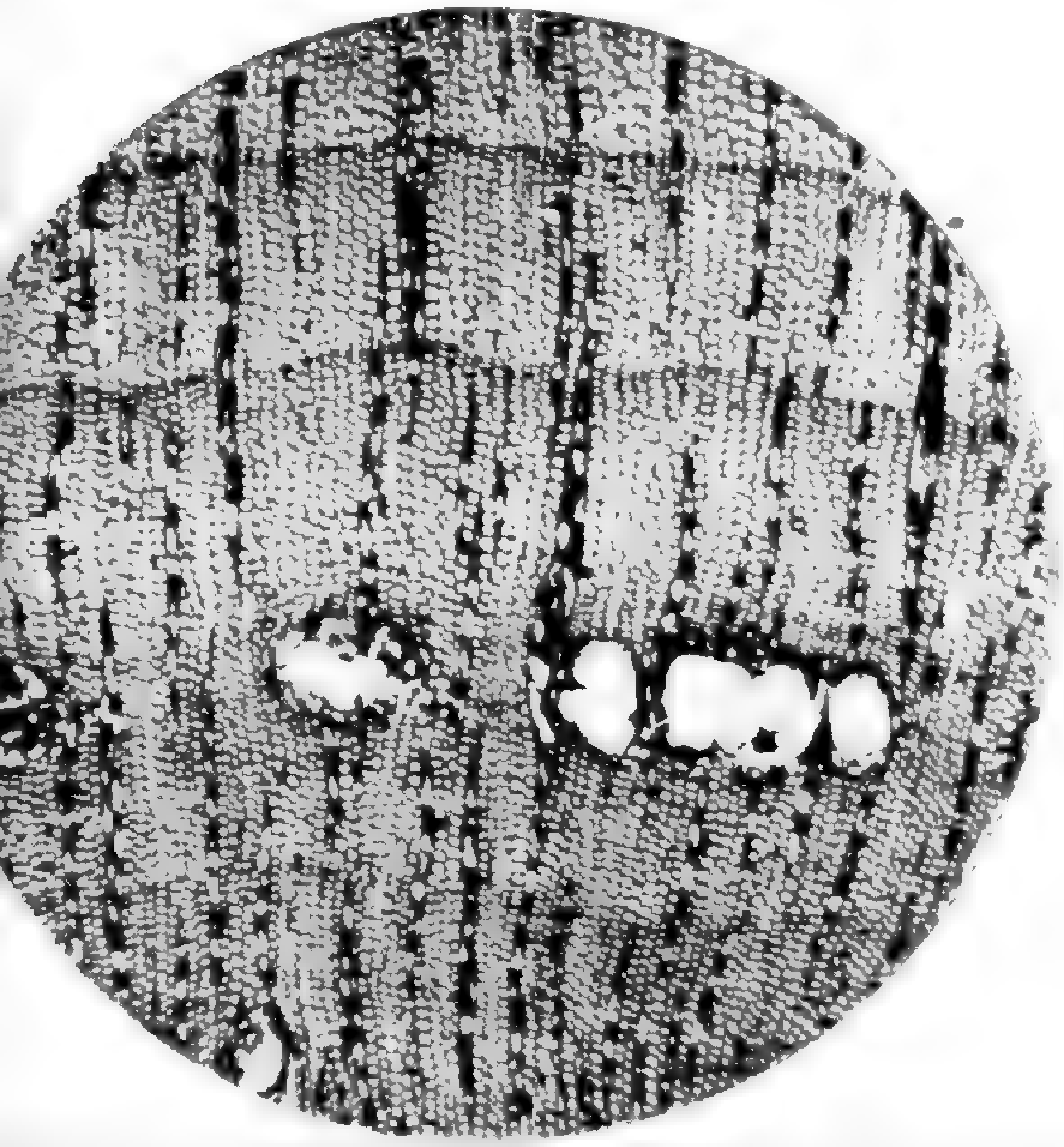
2. These features of difference from modern pines are probably to be regarded as ancestral, since they persist clearly and strongly in the structure of the wood of the cones of the living species.

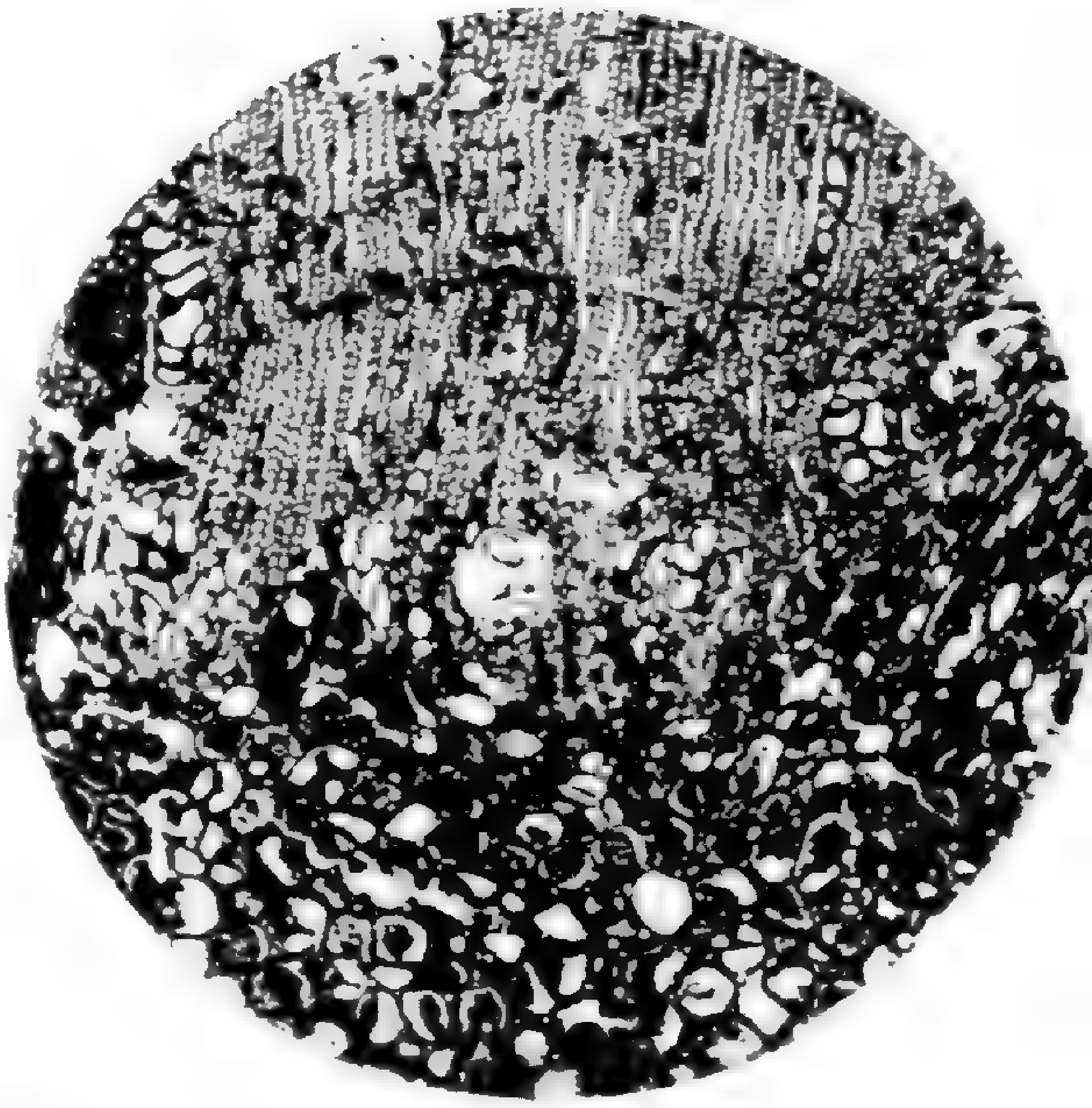
3. The appearance of marginal tracheids in the rays of Pinus is comparatively modern and does not in all probability antedate the Tertiary. It probably explains the greater prosperity of the genus in recent times.

4. Another species of Pityoxylon from Scituate, Mass., has been described, which has the general features of the Pityoxyla of Staten Island. It is not possible, however, to refer it definitely to Pinus, nor is its geological horizon settled.

In conclusion we wish to offer our warm thanks to Dr. HOLLICK for many kindnesses in the matter of securing material.

HARVARD UNIVERSITY.





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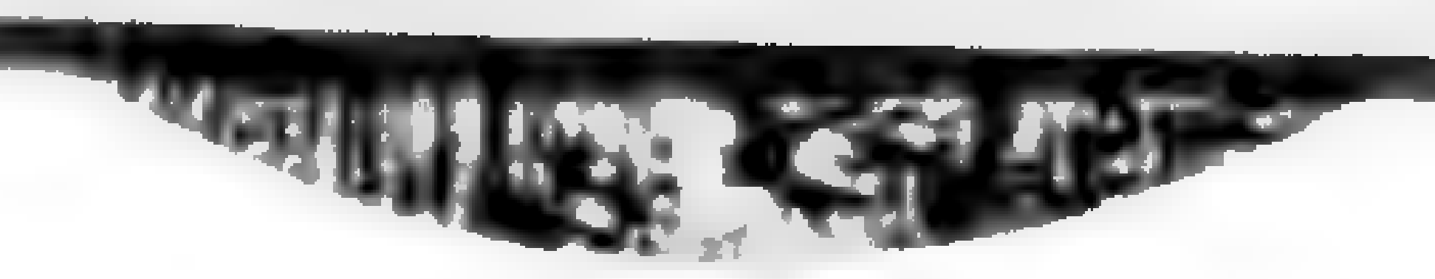

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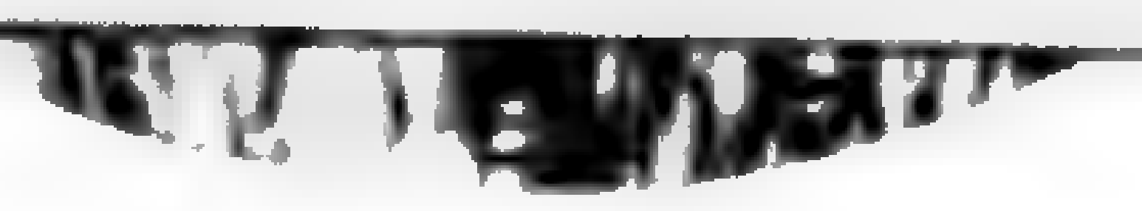

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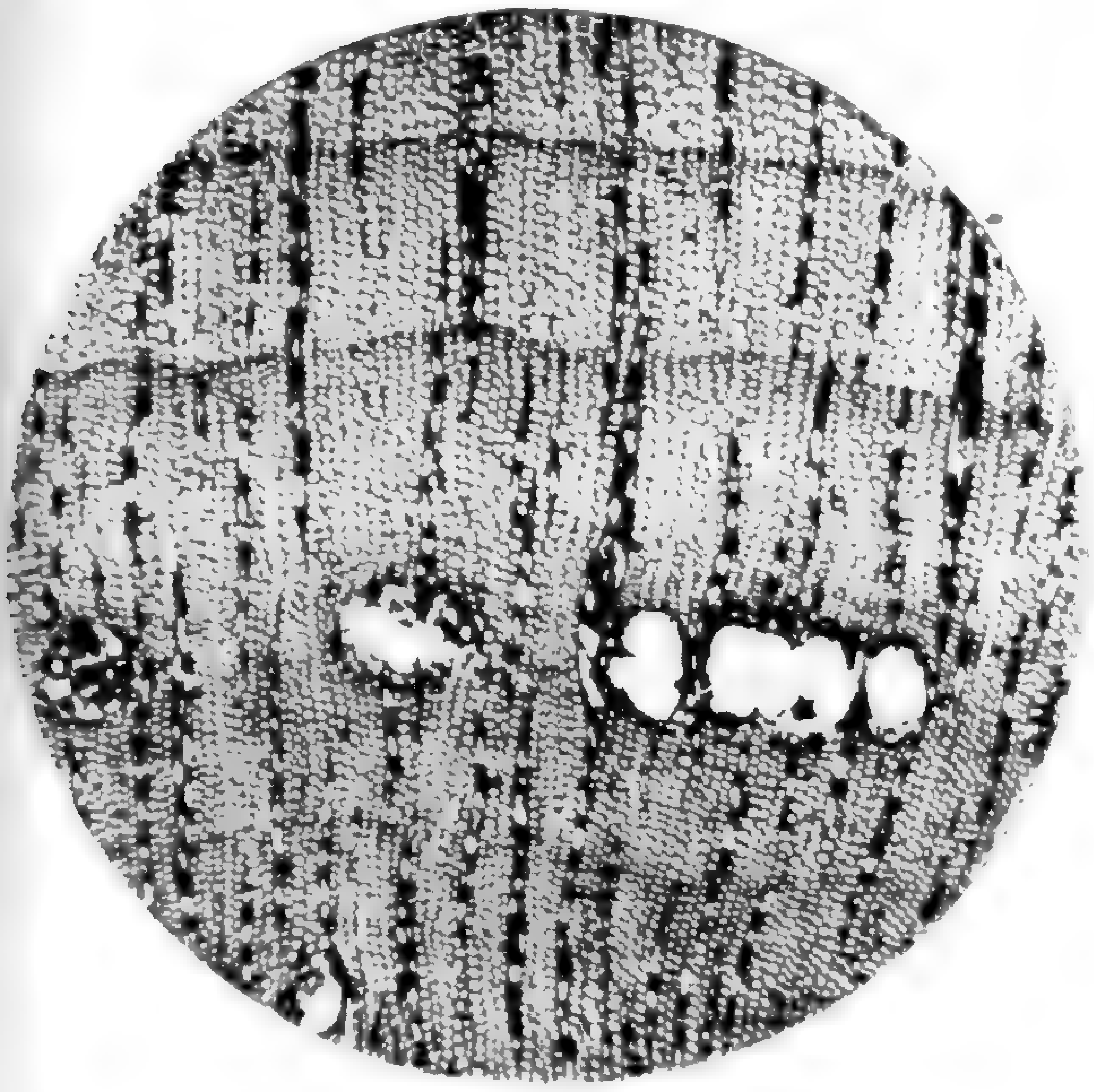

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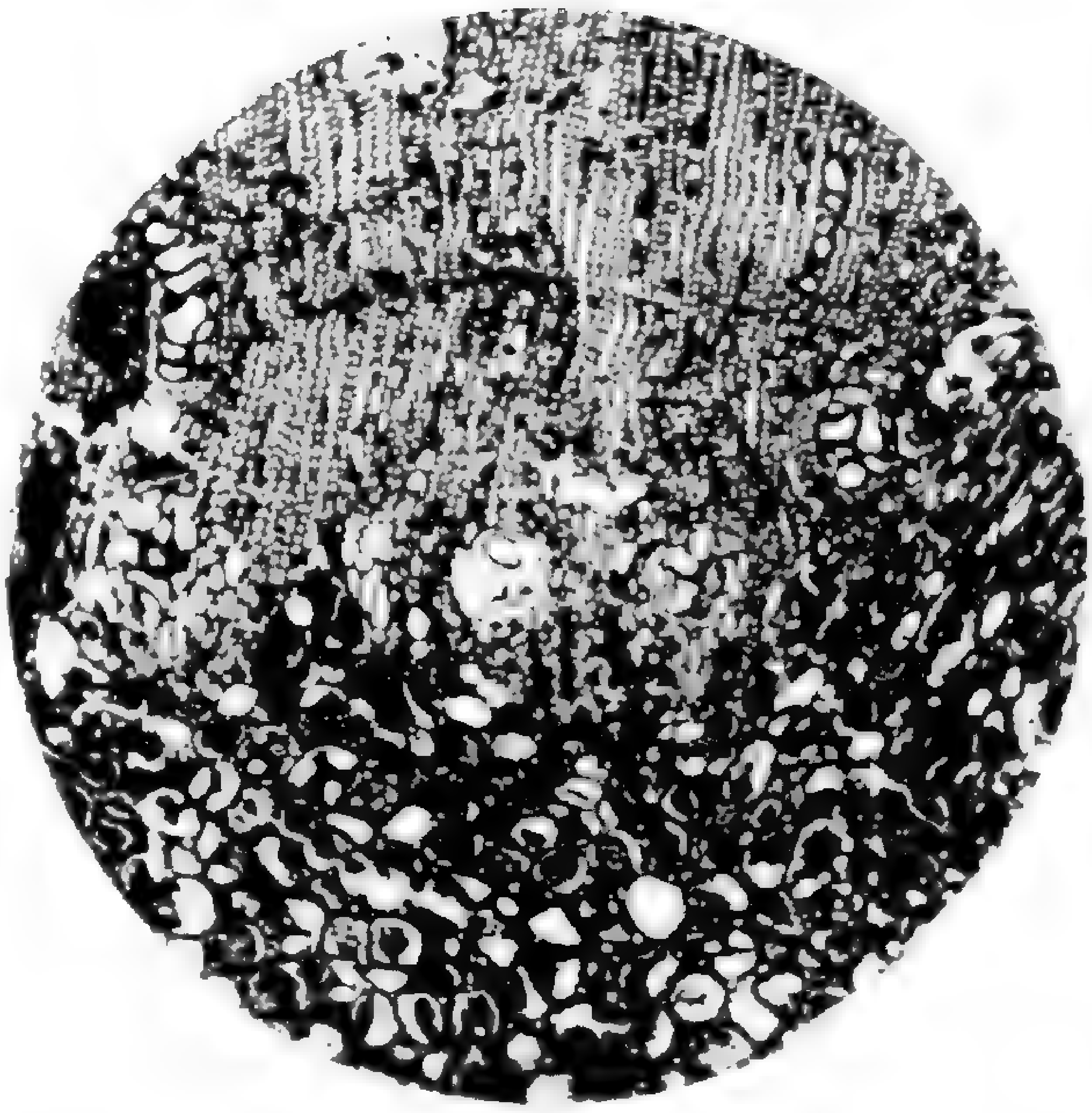

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JEFFREY & CHRYSLER on PITYOXYLA

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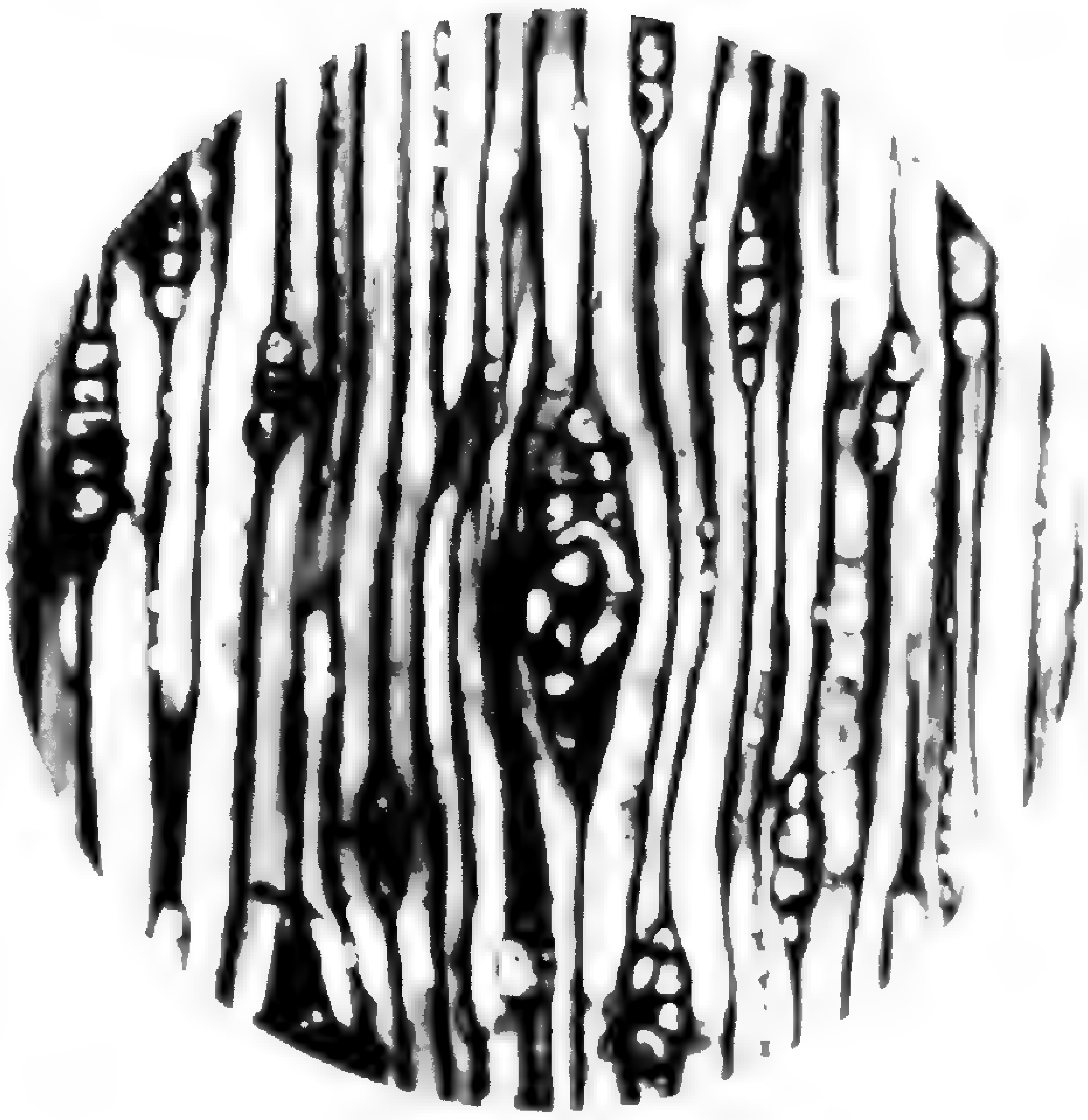

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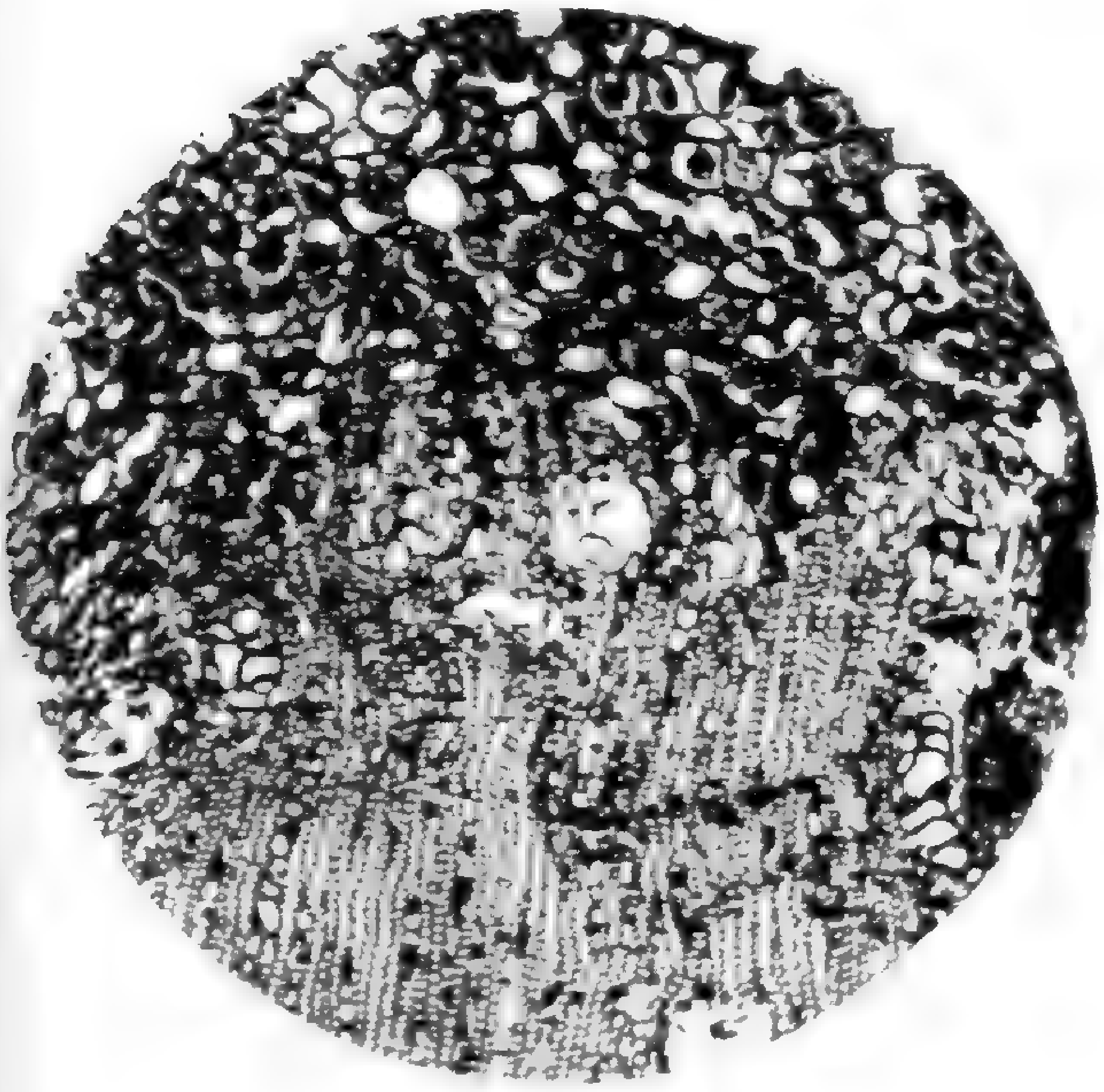

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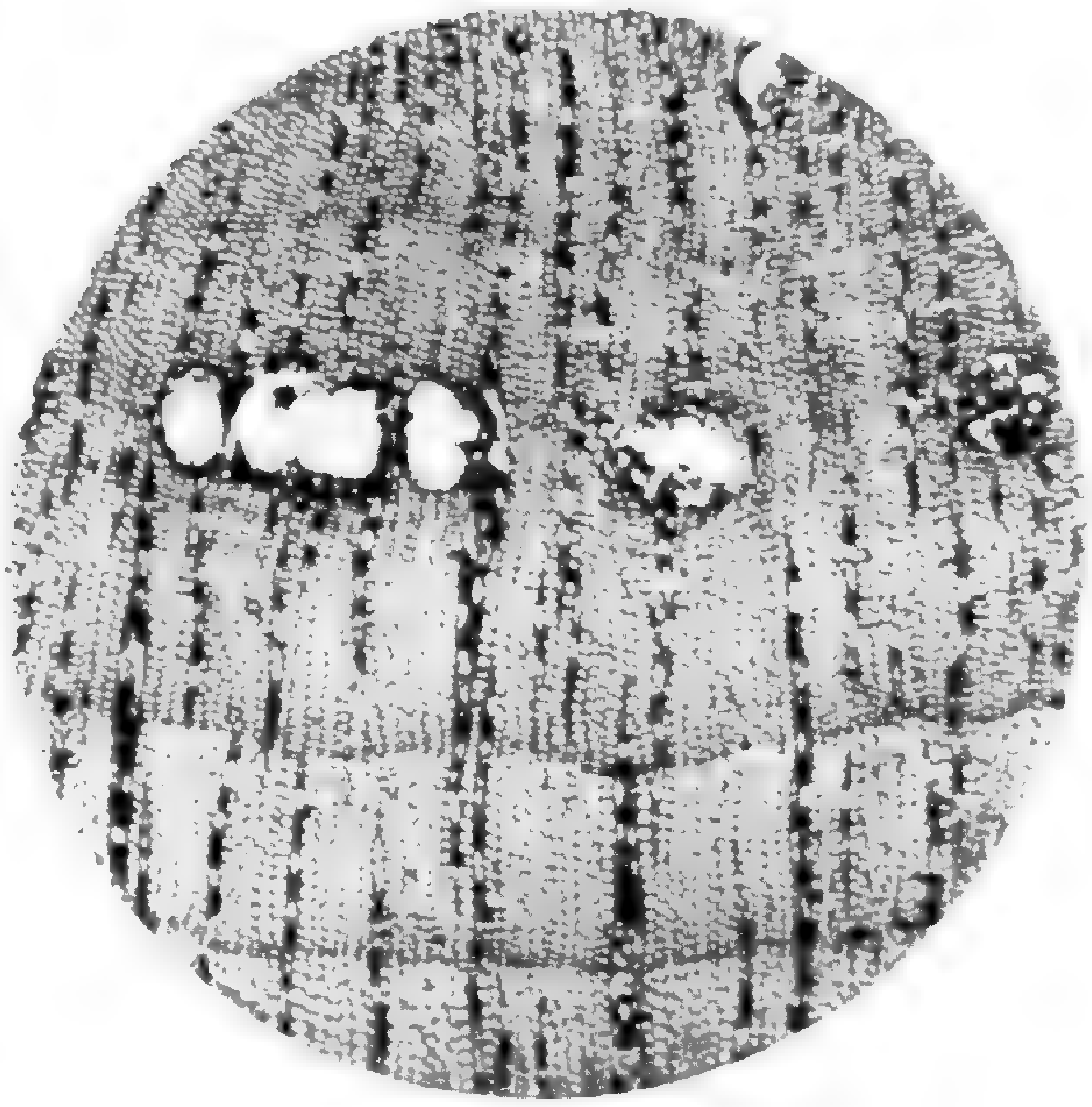

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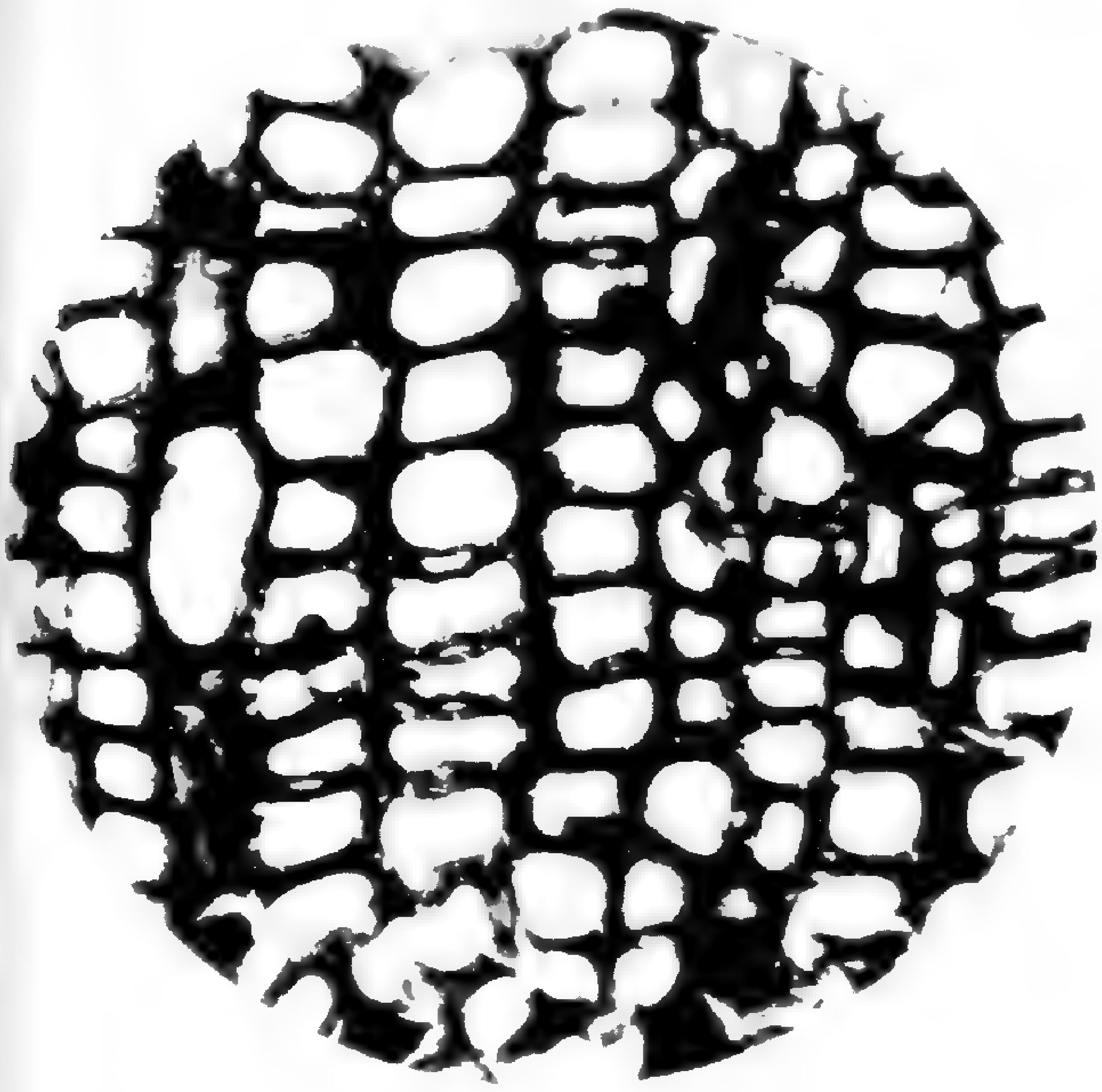
JEFFREY & CHRYSLER on PITYOXYLA



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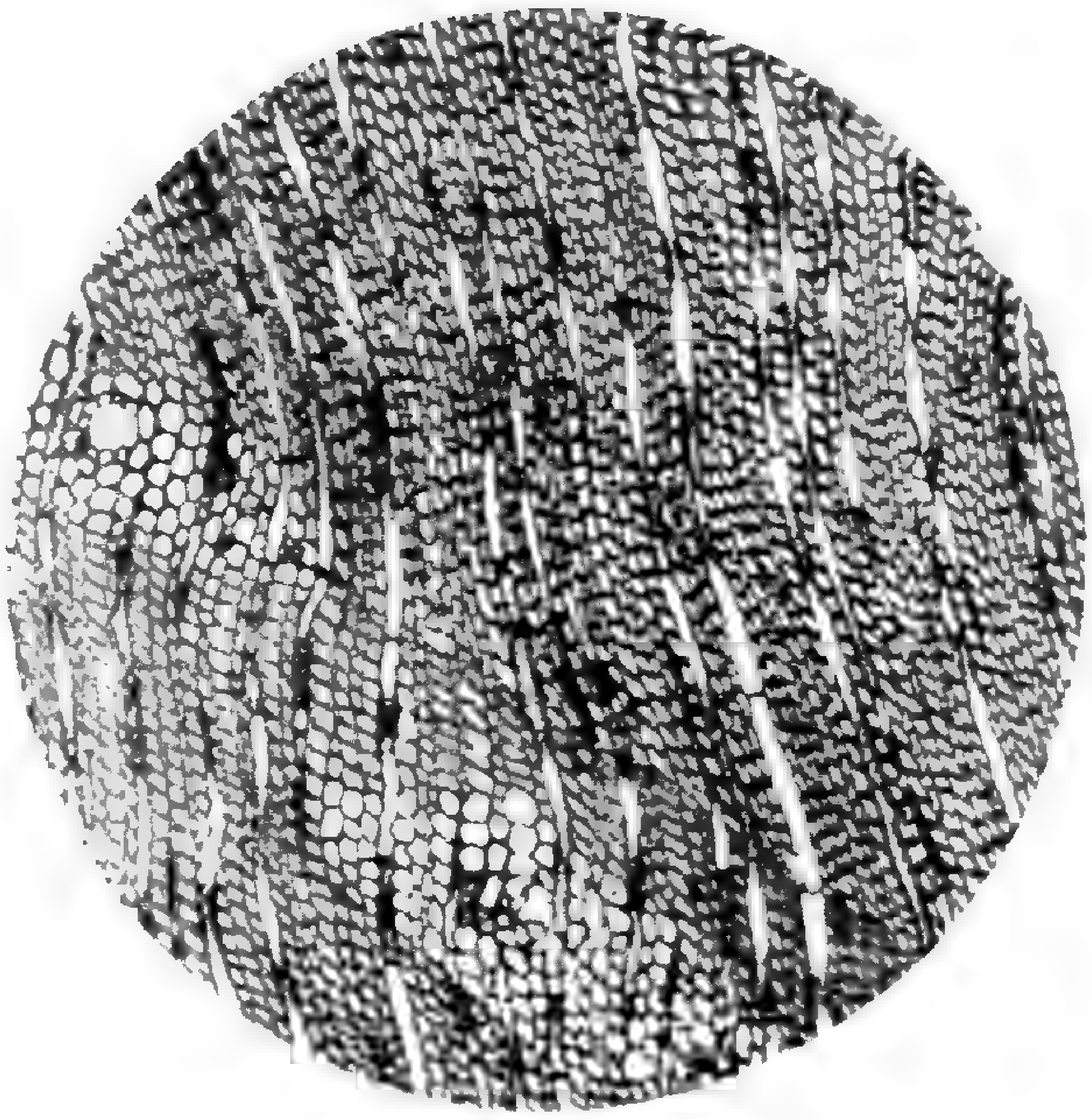

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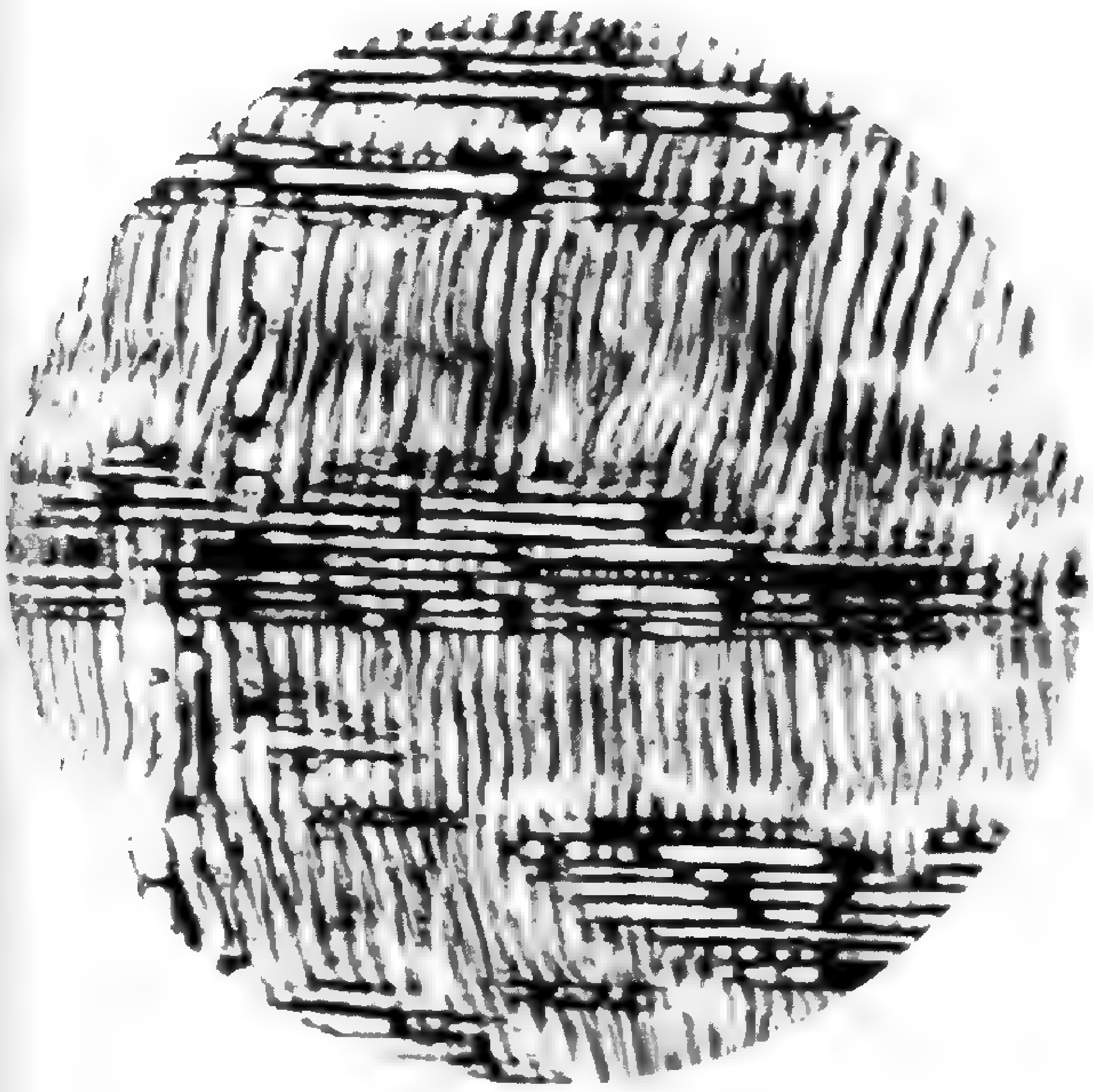

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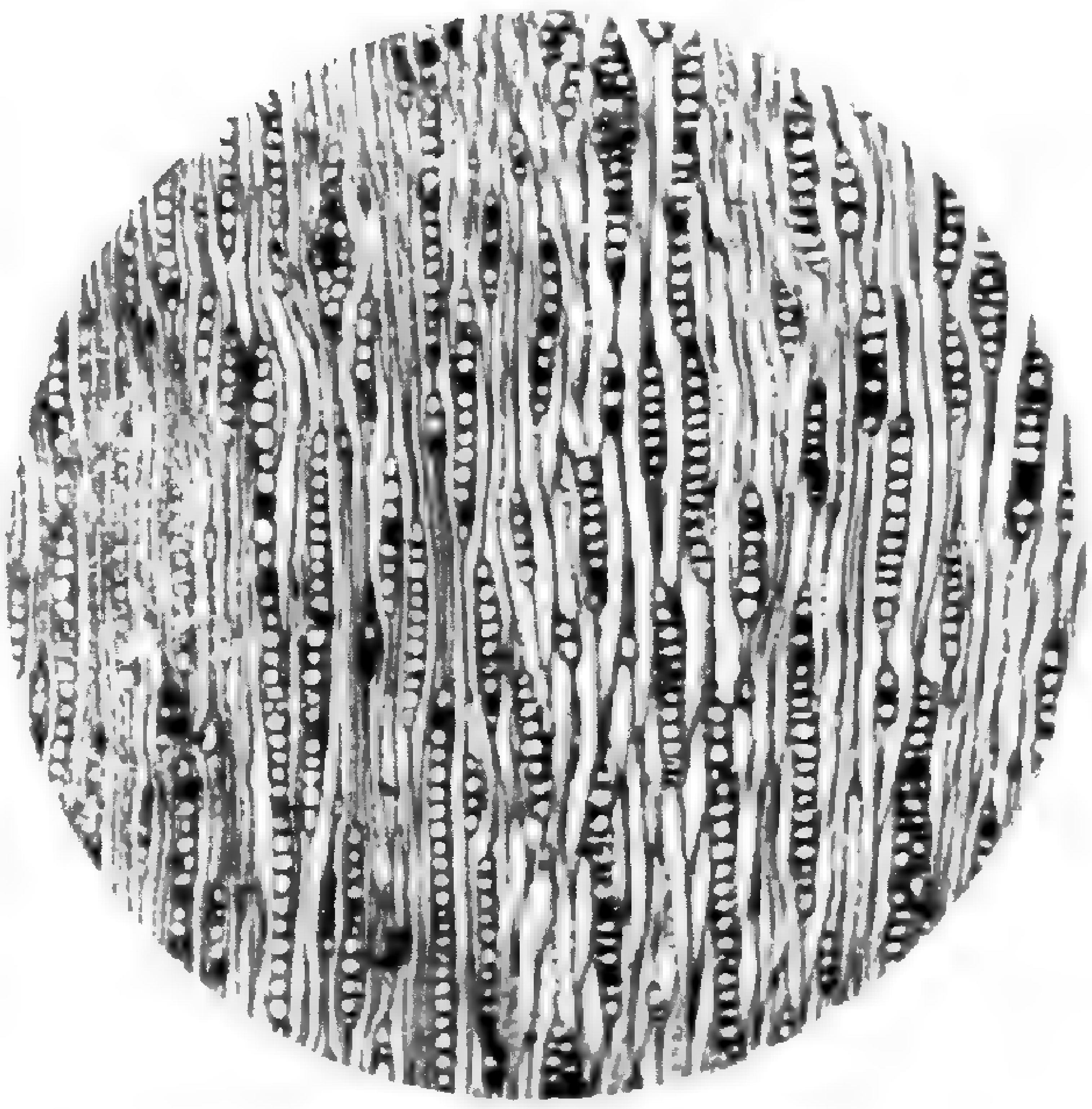

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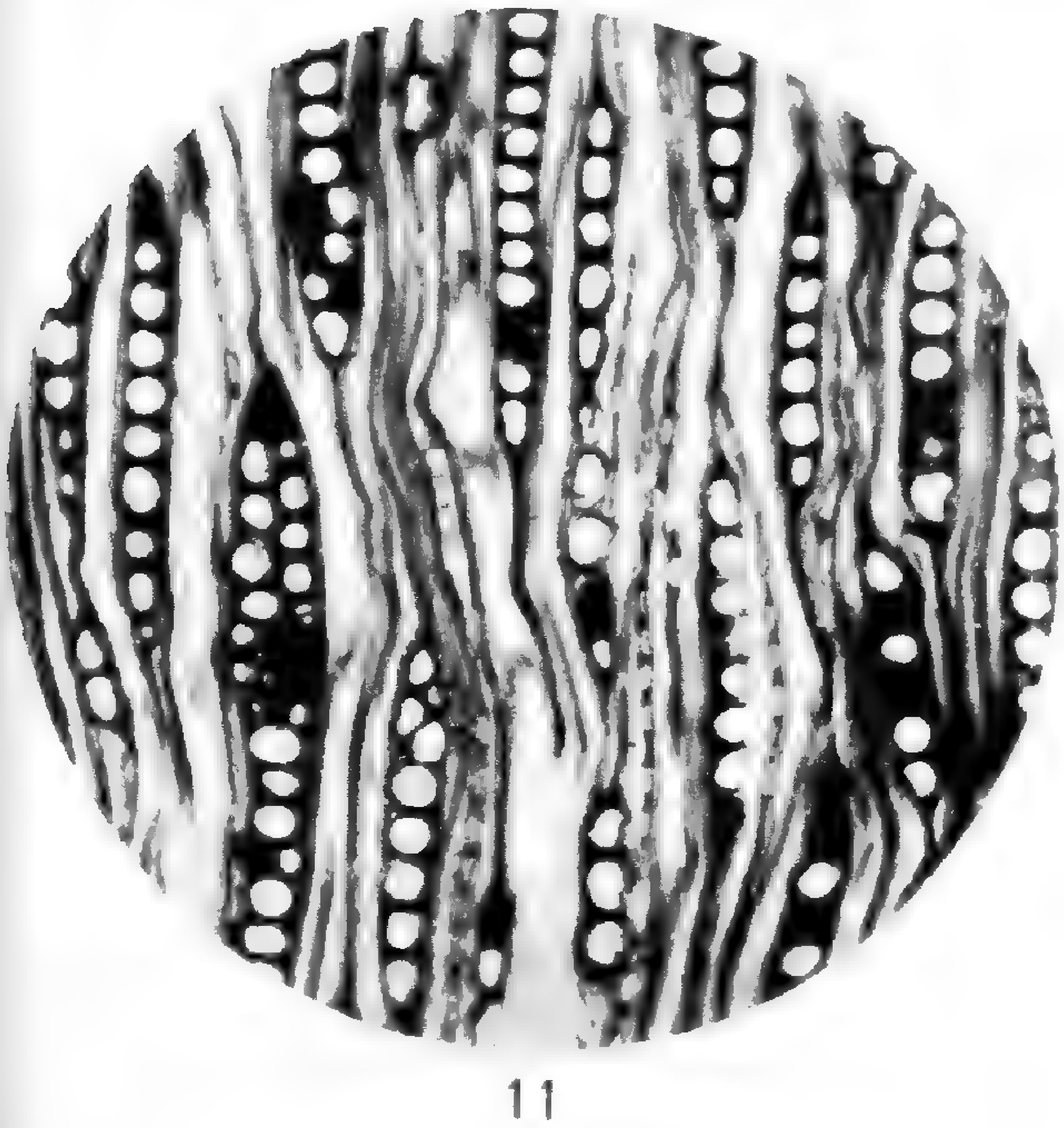

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JEFFREY & CHRYSLER on PITYOXYLA

EXPLANATION OF PLATES I AND II.

PLATE I.

Pityoxylon statenense.

FIG. 1. Transverse section of the wood. ×20.
FIG. 2. Transverse section of the wood near the pith. ×40.
FIG. 3. Radial section. ×60.
FIG. 4. Tangential section. ×60.
FIG. 5. Tangential section. ×180.
FIG. 6. Tangential section. ×180.

PLATE II.

FIG. 7. Transverse section. ×200.

Pityoxylon scituatense.

FIG. 8. Transverse section. ×60.
FIG. 9. Radial section. ×30.
FIG. 10. Tangential section. ×60.
FIG. 11. Tangential section. ×180.
FIG. 12. Tangential section. ×180.

A STUDY OF THE VEGETATION OF THE MESA REGION EAST OF PIKE'S PEAK: THE BOUTELOUA FORMATION.

I. STRUCTURE OF THE FORMATION.

H. L. SHANTZ.

(WITH MAP AND SEVEN FIGURES)

THE region under consideration in this study lies at the base of Pike's Peak and north and west of Colorado Springs. It is the portion known as the Mesa and the Garden of the Gods and contains 3200 to 4000 hectares (*map*). While my attention has been confined largely to this region, studies have been pushed out in all directions, and I have attempted to make myself familiar with the mountain and plains conditions of vegetation, as well as that of the area under consideration. Especial attention was given to the plains which extend eastward from the area first studied.

METHODS.

The methods used in the study of the structure and development of the vegetation, as well as in the study of the physical factors, are those used by CLEMENTS[1] in his ecological studies and need not be mentioned here. The exact methods have been supplemented by careful field notes and photographs. The greatest care was exercised in physical factor readings. The soil samples for the determination of water content were taken with a soil borer, which gave a column of soil reaching to a depth of 15^{cm} and about 2^{cm} in diameter.

Relative humidity readings were taken as near as possible to the surface, and also one meter above. A constant record of relative humidity was obtained by means of the hygrometer at Colorado City, and the isolated readings were compared with this record as well as with the record of the United States Weather Bureau at Colorado Springs. Temperature readings were taken in the soil

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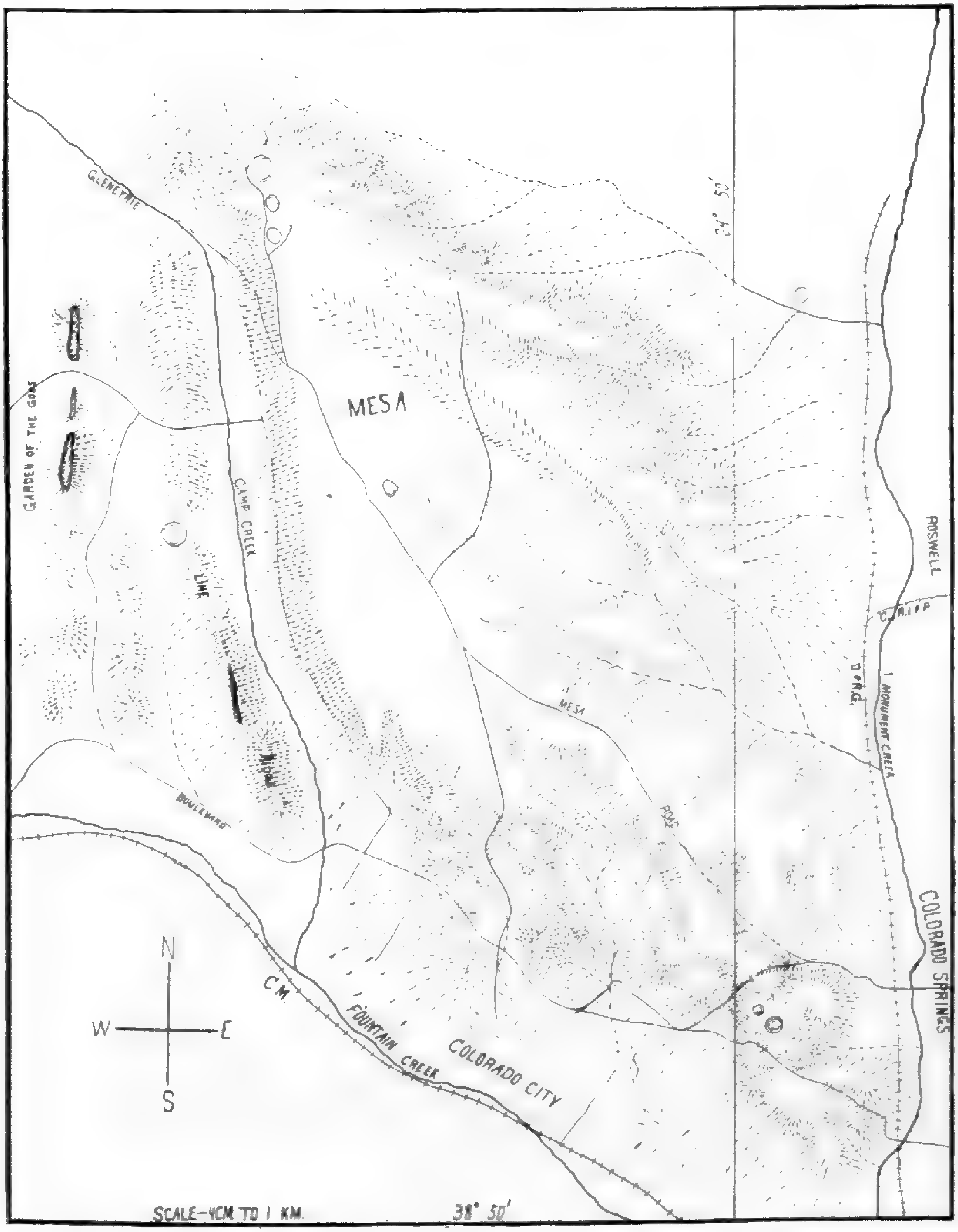
[1] CLEMENTS, F. S., Research methods in ecology. Univ. Pub. Co., Lincoln, Neb. 1905.

at a depth of 15^{cm}, at the surface of the soil, on the plant, at 10^{cm} above the soil, and finally 1^{m} above the surface. A constant record was taken by means of a thermograph, and the records of the Weather Bureau were also made use of to check the results thus obtained.



MAP.

In the measurement of light the writer has used the ordinary photometric method, but has used the standard derived from the candle power. Solio paper was exposed to a standard candle for

15 hours at a distance of 10^{cm}. The Hefner-Alteneck lamp burning acetate of amyl was used as a standard. The diameter of the wick was 8^{mm} and the height of the flame was 40^{mm}. The shade produced on the Solio paper was used as a standard and copied in permanent colors. Strips of the same sheet of Solio used to make the standard were exposed and the time required to produce the standard tint recorded. This gave mathematical data and a very simple means of comparing light intensities. The light at the June solstice was about 4.5 seconds. All exposures were made parallel to the soil surface.

In the diagnosis of the habitat I have given the figures found to apply during the time studied. Rainfall, temperature, wind, and humidity are averaged for four seasons. The data in water content are based on a single season's work, but on a great many readings. The data on non-available water were obtained by taking the soil samples at the time when the plants were dying. This water varies not only with the species, but also with the individual plants. The data as collected were largely at the time of the dying of *Boebera papposa*, *Salvia lanceolata*, *Helianthus annuus*, *Verbesina encelioides*, and *Solanum rostratum*, mostly during the latter part of the aestival period; and these results are given in the other diagnoses, since at other times it was impossible under natural conditions to obtain such data. Available water is expressed in grams to 100 grams of dry soil. The duration of each aspect, as well as many of the factors which are definitely stated, varies from year to year.

The species lists are arranged to give an idea of the relative importance of the species under each heading, the most important species appearing first. The lists without the species in parentheses are for the Mesa region only. Important species of the formation which do not occur in the Mesa region are included in parentheses. They will be taken up under the general discussion. In the lists important parasitic fungi always appear after the species upon which they occur.

Within the formation the following are the terms applied to the plant associations: *consocies*, or areas which are dominated by a facies of the formation and which at all periods give the characteristic stamp to the vegetation; *societies*, or minor divisions, characterized by principal species and dominant usually over smaller areas and only during the aspect in which they occur; *communities*, or smaller associations, usually of secondary species.

GEOLOGY.

The eastern base of the Rocky Mountains shows a great many rock systems which are upturned and all come to the surface in or near this region. Lying on the Archean granite, which forms the mountains at the west, is found a Cambrian red sandstone, gravel or lime. The Silurian or Manitou limestone lies next, followed by the reddish gray quartzite sandstone of the Carboniferous. East of this the Garden of the Gods is formed by the great red sandstone outcrop which is placed in the Permian or in the Triassic—authorities differ. The Jurassic, which lies next, is followed by the Cretaceous rock system, represented by the following epochs. The lowest is of the Dakota—the white sandstone ridge or hogback, and the great sandstone ledges. Lying next and buried in most places under the talus of the latter is the Benton shale. The most eastern of the series of hogbacks marks the outcrop of the Niobrara limestone. The Fort Pierre shale is found in many places east of the lime ridge and underlies the whole Mesa region. Lying above this is found the recent Quaternary deposit of gravel of granitic origin.

The sedimentary deposits underlie the entire Great Plains region, but in most places are covered by the more recent wash from the mountains. For the geological development and structure of the Great Plains, as well as for a description of the topography and climate, the reader is referred to the exceedingly interesting publication by JOHNSON.[2] The following quotation from this source (p. 612) gives a very clear idea of the origin of the plains.

> The Great Plains are of such vast dimensions it is only in imagination that they can be regarded as a foot slope to the Rocky Mountains. However, in the sense that, superficially, ranging down to several hundred feet in depth, they have been built to a smooth surface by mountain waste, stream-spread to great distances, they have this character. At the base of the mountains the Plains mass has a thickness, to sea level, of several thousand feet. It is made up in

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[2] JOHNSON, W. D., The high plains and their utilization. Ann. Rept. U. S. Geol. Survey **21**⁴: 601–741. 1899–1900.

the main of marine-rock sheets with a general inclination eastward, due to broad regional tilting, in which the plains and mountains have shared together.

But the present surface grade of the Plains is not that of the original tilting. The surface has undergone a series of transformations. These have all been accomplished by the eastward-flowing streams from the mountains. In a first stage the mountain streams, traversing the Plains, cut into the smooth structural slope, and produced a topography of parallel broad valleys and ridges. In a second stage they ceased to cut, depositing instead, and refilling the valleys they had excavated, even burying the intervening ridges, to a smooth upper surface. The original surface was a product of deformation, the second of a destructive process of stream erosion, the third a product of stream deposit and construction, involving the spreading of a waste sheet to great distances and a uniform level, and to a depth over the greater valleys often of several hundred feet. In the final and present stage, virtually the same streams have returned to the earlier destructive habit, and erosion has in large part carried away the high level plain of stream construction. About midway of the long slope, in the north-south irregular belt, large uneroded fragments of the smooth constructional plain remain. As we have seen above, these fragments constitute the High Plains.

FIG. 1.—Gully on the east side of the Mesa; alternation between thicket and grass formation.

PHYSIOGRAPHY AND SOILS.

The exposure of the Mesa is southeast, the grade being about 18^{m} to the km. The northwest portion, which is the highest, has an elevation of 1889^{m}. On the east and south sides of this Mesa the water has cut deep gullies (*fig. 1*), which appear older on the south than on the east, the slope being more gradual and the soil more stable. The east side of the Mesa is bounded by a low region largely of clay sand, which slopes gradually to Monument Creek. On the north side there is a less elevated region which, however, does not differ markedly from the Mesa itself. On the west side is Camp Creek, which has cut down into the Fort Pierre clay.

The soil of the Mesa is a gravel mixed with a limited amount of clay and humus. The gullies and edges of the Mesa are made up of Ft. Pierre clay, which is in places mixed to some extent with the Quaternary gravel which lies above it.

CLIMATE.

Rainfall.—The greatest amount of rain is during the growing season, the fall and winter, as a rule, receiving very little. As a result the vegetation is not protected in the least by snow during winter, nor is there a sufficient amount of water to retard the evaporation from the aerial parts of the plant. There is, as a rule, considerable rain during the summer months from May to September, but often the rainy season is much shorter, covering, as it did in 1903, only June, July, and August. The rainfall is about 32 to 43^{cm}, but because of the unequal distribution throughout the year, this affords a rather luxuriant summer growth. This seasonal variation in rainfall is best illustrated by the following table, which gives the rainfall in centimeters.

Year	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1901	0.15	0.17	2.97	4.67	9.52	....	....	5.68	5.58	1.24	0.02	0.45	.....
1902	0.20	0.35	1.01	2.07	13.28	3.96	4.21	6.83	0.40	0.38	0.05	0.55	33.29
1903	0.15	1.77	0.93	2.41	1.57	12.95	1.07	6.29	1.52	0.86	2.03	0.63	32.18
1904	0.27	0.48	0.15	0.58	10.46	9.86	7.87	6.35	5.25	0.67	Trace	1.14	43.08

There is also a daily variation in rainfall which is of some importance to the plant. The relative humidity, of course, is much higher during the night than it is during the day, and on this account rain which falls in the afternoon and leaves the ground wet at night sinks into the soil and does the plant much more good than does that which is followed by a clear sky and rapid evaporation.

A study of the rainfall record shows that much more rain falls during the afternoon than during the forenoon. During the months of May, June, July, and August, 1904, 72 per cent. of the rain fell in the afternoon; while 71 per cent. of the hours during which rain was falling were in the afternoon. The sunshine record (*fig. 6*) also makes this plain.

Relative humidity.—A deposit of dew is extremely rare. The relative humidity therefore seldom reaches 100 per cent. except during showers. During the day it is generally low, often being as low as 1 per cent.; on account of this, rain or snow is soon evaporated. The relative humidity is especially low during winter when there is little rain and when during the day the temperature often rises to 16°–20° C. The following table gives the relative humidity for each month of the year 1904; and *fig. 2* illustrates the daily variation.

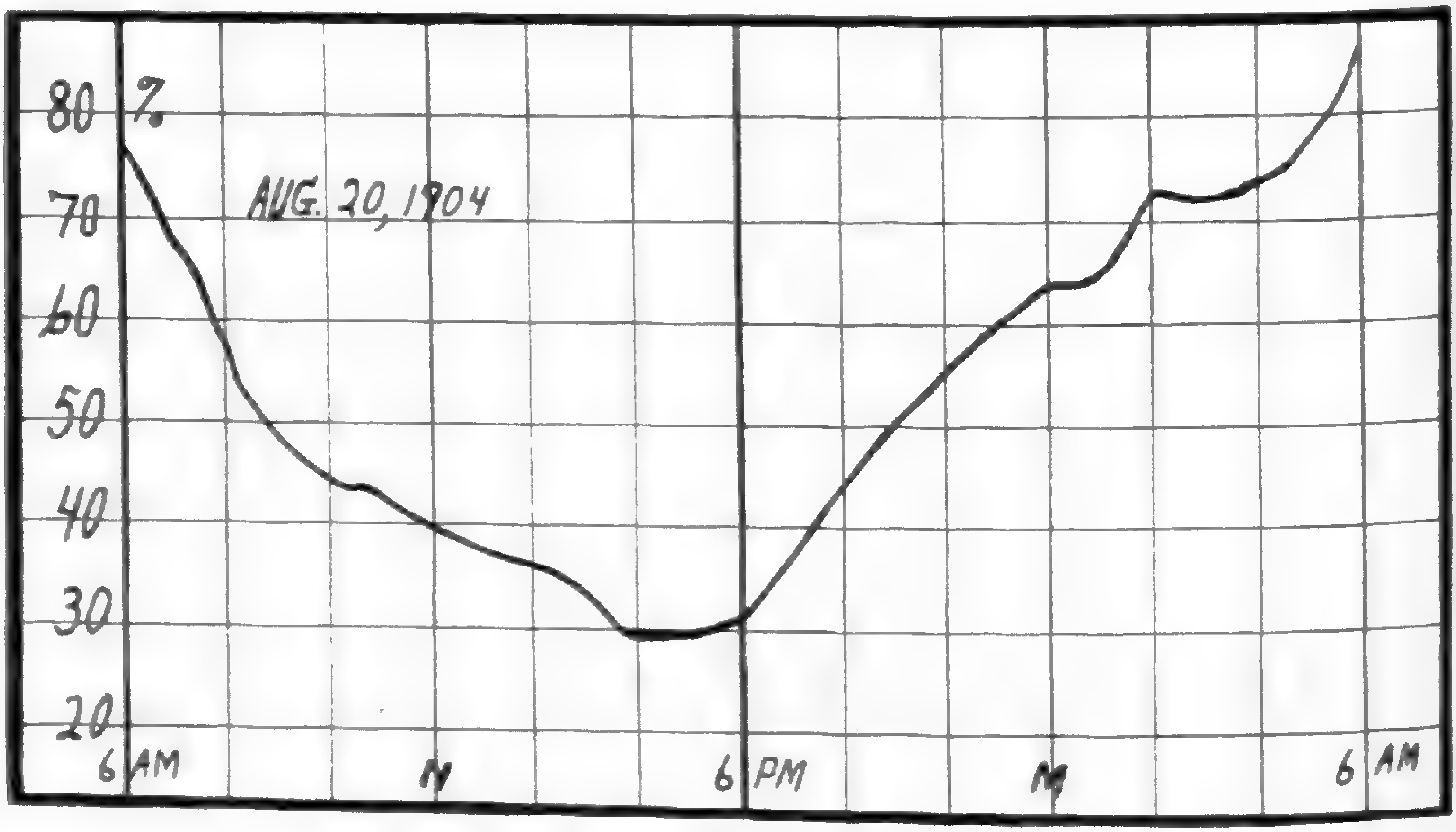

FIG. 2.—Daily variation in relative humidity.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Maximum....	90	89	100	100	100	94	90	95	100	100	89	100
Minimum....	1	8	6	1	11	12	9	21	13	12	12	5
Average......	47	41	42	44	55	54	51	55	44	52	43	49

Wind.—The chief importance of wind is its effect upon the transpiration of the plant and upon the water content of the soil. The following are the velocities in hm. per hour for the different months of the year 1904: Jan. 4.6; Feb. 3.3; Mar. 5.7; Apr. 6.09; May 4.7; June 3.7; July 3.5; Aug. 3.2; Sept. 3.7; Oct. 3.8; Nov. 4.04; Dec. 4.3.

Temperature.—Extremes in temperature do not occur. The summer temperature is seldom above 32° C., and the winter temperature is seldom −18° C. The maximum temperature recorded during the four years 1901–4 was 36°.6 C., and the minimum for the same period −28°.3 C. The following temperatures are for the year 1904.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Maximum	17.7	21.6	20.5	22.8	25.5	28.3	31.6	29.4	28.3	23.3	19.3	18.8
Minimum	−18.3	−18.3	−14.4	−9.4	−1.1	2.7	6.1	7.2	5.5	−5.5	−5.5	−20.5
Mean	−2.8	2.2	3.9	7.7	11.5	14.9	18.2	19.5	17.3	9.4	5.1	0.2

The mean temperature is derived from the daily maximum and minimum. The daily variation may best be shown by curves from the thermograph (*fig. 3*).

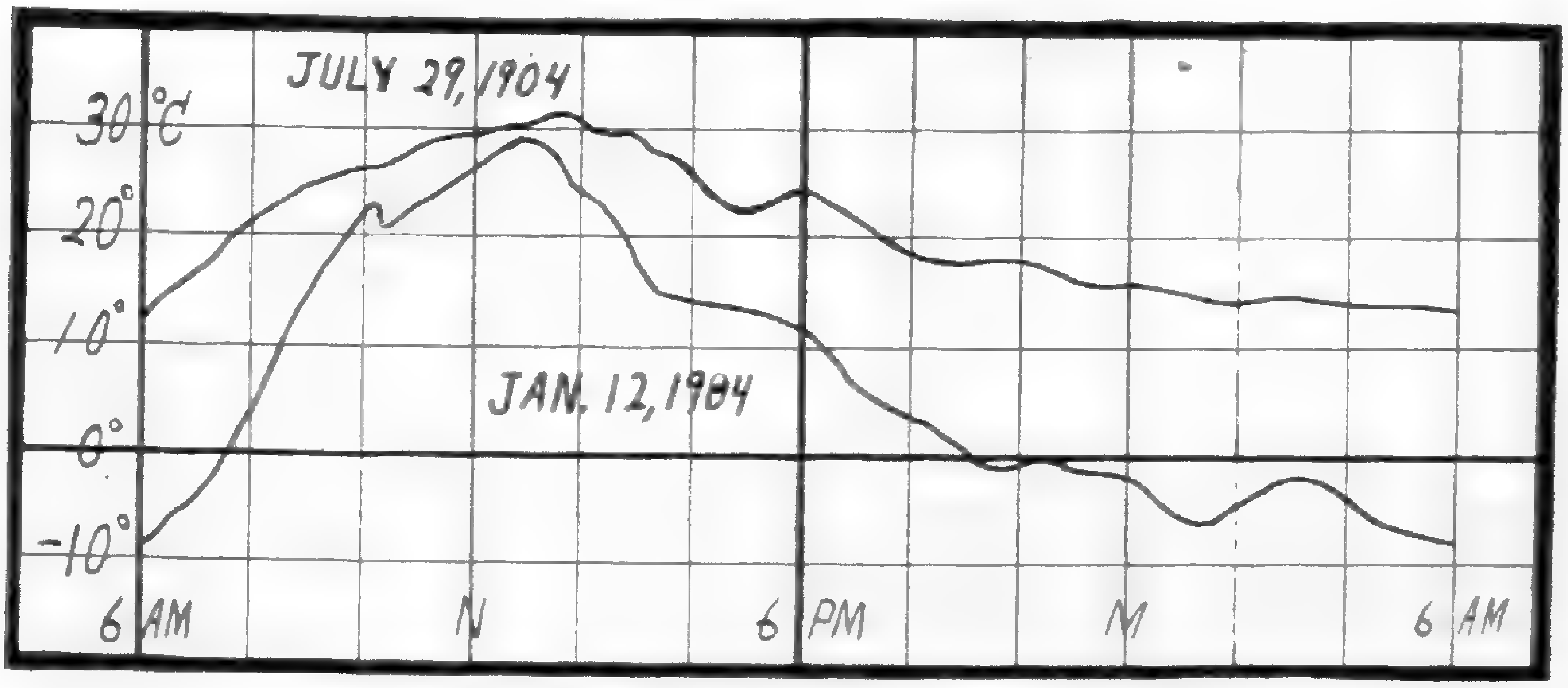

FIG. 3.—Daily variation in temperature.

A comparison of these curves will show clearly how much greater is the daily range in winter than in summer. The curve for January 12, 1901, rises higher than the typical winter curve, but is otherwise normal.

A series of curves showing the variation in temperature between the soil, soil surface, plant surface, 10^{cm} above the soil surface, and 1^{m} above will serve to show how different are the conditions of temperature under which the plant lives from those ordinarily recorded (*fig. 4*). At the top of the figure is given the sunshine record, together with the light intensity for each hour of the day. The water content was determined twice, as recorded in the figure. The plant surface temperature record was taken on a mat of *Bouteloua oligostachya*, and the quadrat was situated on a south slope.

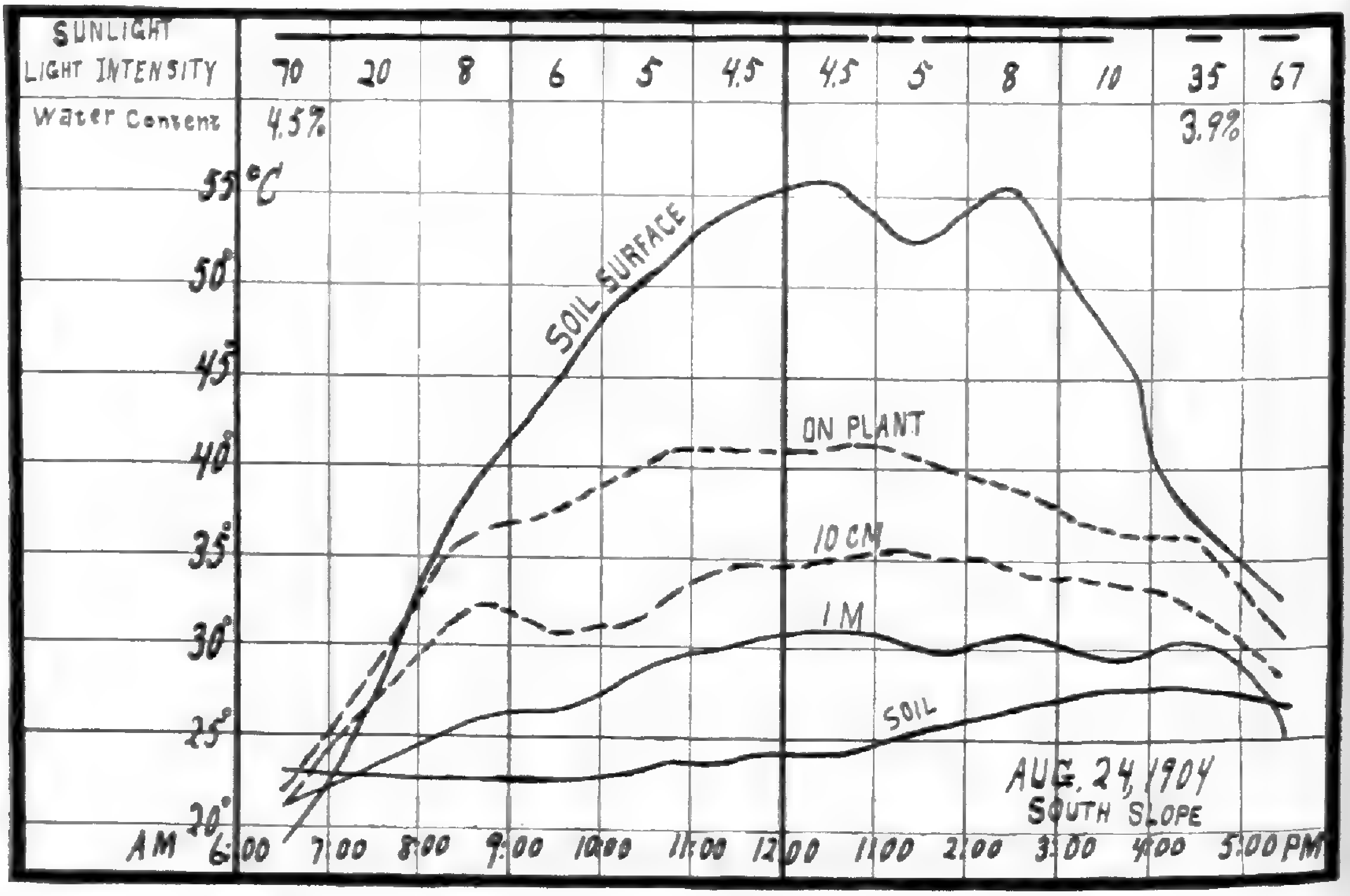

FIG. 4.—Variation in temperature at different levels.

The extreme conditions at the surface of the soil may account to some extent for the dying of the lower stem leaves, so often noted among perennials as well as annuals.

Simultaneous readings on north, south, east, and west slopes give the curves for soil and soil surface temperatures shown in *fig. 5*. The water content was recorded twice in each quadrat and is also given in the figure; curves of soil temperature are given at the bottom of the figure. Some idea of the temperature at the various levels may be obtained by comparing these curves with those of *fig. 4*. The readings shown by *figs. 4* and *5* are simultaneous.

Light.—The sunshine records taken show 51 to 80 per cent. of possible sunshine. The difference between possible sunshine for the forenoon and afternoon is seven to nine hours per month during

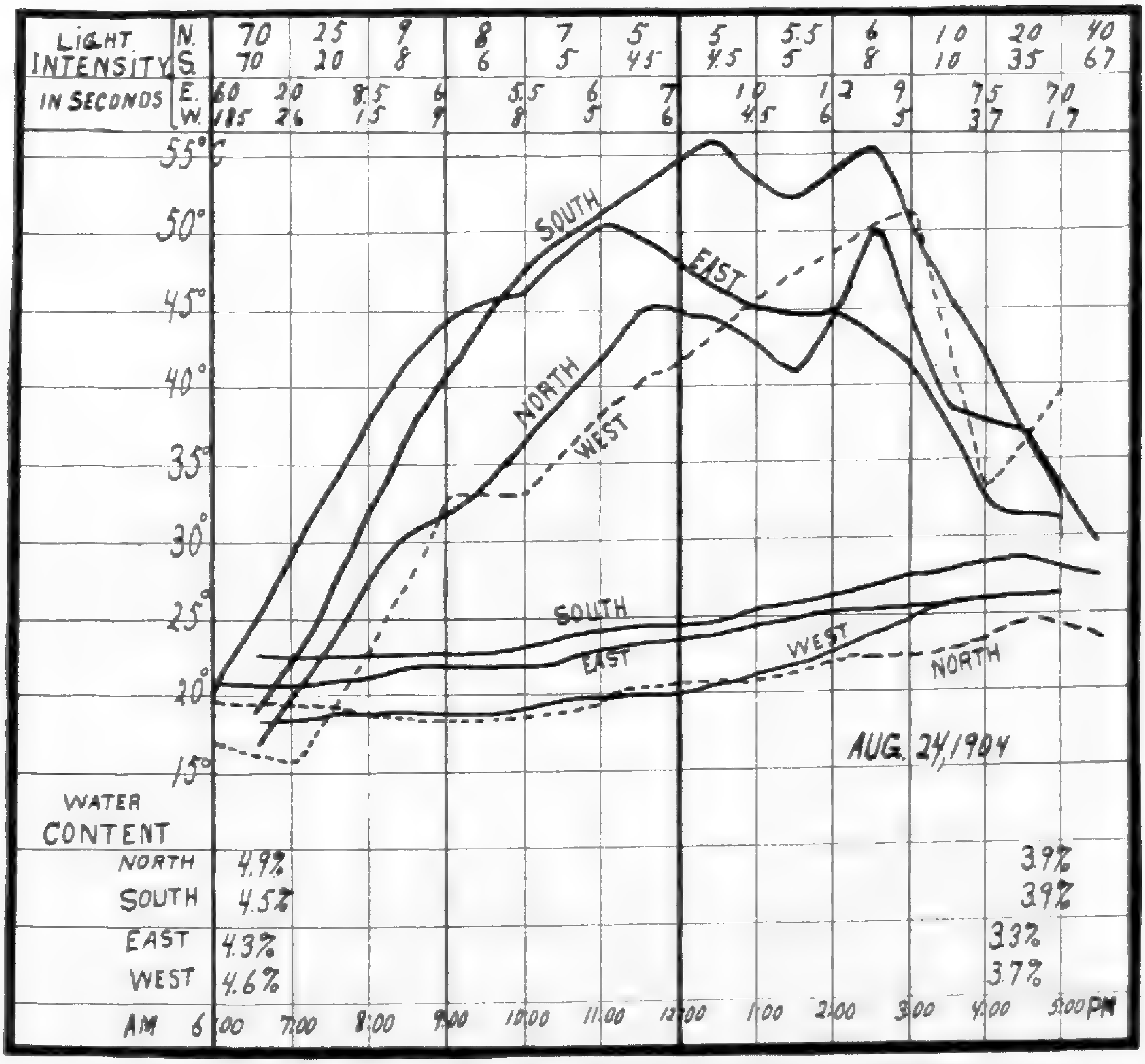

FIG. 5.—Variation in temperature and light intensity on different slopes.

the period of growth. This is due to the mountains which shorten the period of illumination for the afternoon. The rains and cloudy

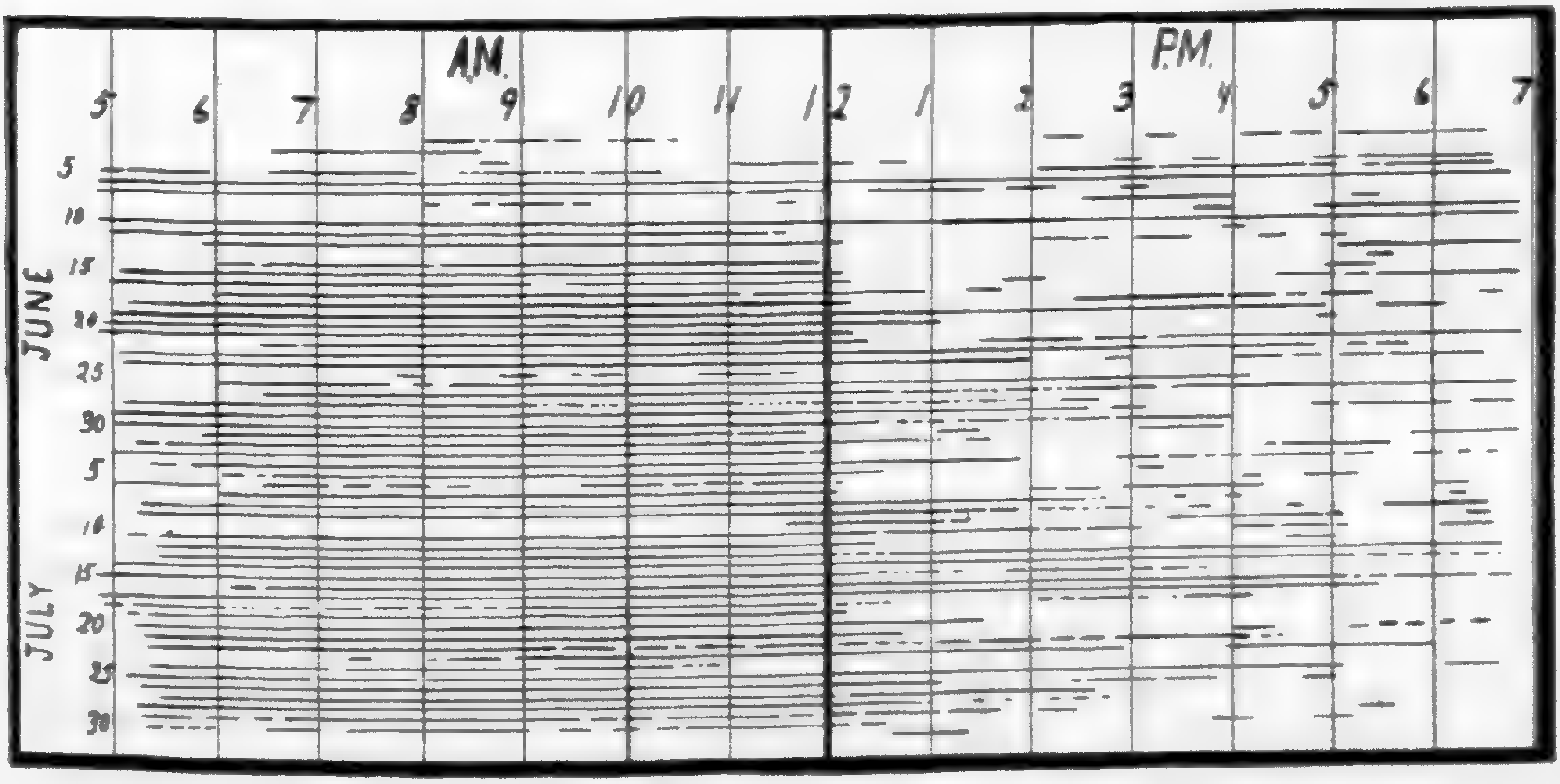

FIG. 6.—Sunshine record.

sky occur most frequently during the afternoon, which on this account also receives much less sun than does the forenoon. The record for sunshine for June and July 1904 makes this clear (*fig. 6*).

The difference in the light received by the east and west slopes, together with the resulting differences in temperature, relative humidity, and water content, is of importance in explaining the vegetation of these exposures.

The Bouteloua (grama grass) formation.

This formation occupies practically the whole Mesa region and the low land surrounding it. It extends for many miles north, south, and east, but no attempt has been made to determine its limits. It seems to be the formation most typical of the high plains and extends eastward far into western Kansas and Nebraska.

The season of growth may be divided into two periods: the vernal, or in this case the spring and early summer period; and the aestival, or late summer and autumn period. Each of these grand periods may be divided into two periods: the first into the prevernal and vernal, the second into the aestival and autumnal.

PREVERNAL ASPECT.

Habitat.—Physical and available water content very low. Rainfall 0.48–2.43^{cm} (April 1904, 4.68^{cm}); av. daily, 0.008^{cm}. Relative humidity: mean, 44 per cent.; range 1–100 per cent. Wind 6.09^{hm} per hour. Temperature: mean 7°.2 C.; mean max. 14°.4 C.; mean min. 0° C.; range −11°.1 to 25° C.; soil, 13° C. Light duration 66 per cent., exposure varied, cover open, soil clay to gravel. Duration April.

PRINCIPAL SPECIES: Leucrocrinum montanum Nutt., Townsendia exscapa (Richards) Porter, Pulsatilla hirsutissima (Pursh) Britton.

SECONDARY SPECIES: Cymopterus acaulis (Pursh) Rydb., Phellopterus montanus Nutt.

The winter conditions are xerophytic, there being very little rain and seldom a snow cover. The mean relative humidity is low—40 to 50 per cent., and sometimes falling as low as 1 per cent. The temperature in winter rarely falls below −18° C. and often rises above 16° C. The records show 56 per cent. of possible sunshine, and the surface of the soil rises to a temperature much higher than that of the air.

To understand and explain the appearance of the vernal and prevernal flora it is necessary to take into account the winter condition. The water content is low at the time of the appearance of the first flowers. The north slopes have a higher percentage of water than the other exposures, and although the temperature is lower it is here that the greatest number of spring flowers are produced. Only very resistant species seem to be able to survive the long dry winter and produce flowers in the spring on the south slopes. The high temperature which the soil of this exposure reaches during the winter would surely start growth at a period when such development would be disastrous to the life of the plant. This probably explains the abundance of the north slope vernal flora and the paucity of the south slope flora during the same period.

Before the spring rains have begun, at the end of the long dry period, this prevernal flora makes its appearance. These plants are never very abundant on the Mesa proper, but appear in great numbers on the hillsides. In each case the flowers appear either without any foliage or with very little.

The most prominent society of this period is the Pulsatilla society, characterized by P. *hirsutissima.* Its distribution within the region studied is limited to the north slopes and it is never found on the south slopes. The plants are often very numerous and constitute almost the only growing vegetation of this period; forming a zone along the north and east slopes of the Mesa which is only interrupted at places of south or southern exposure.

Leucocrinum montanum forms a society which is less exclusive than the former and is at the same time less distinct. It reaches its maximum development on north crests, but may occur in almost any situation except the south exposure. Over the greater part of the Mesa *L. montanum* is mingled with *Townsendia exscapa,* and these two plants constitute the only vegetation of the Mesa top at this period.

Cymopterus acaulis and *Phellopterus montanus* seldom form communities. In their distribution they show a marked alternation, *C. acaulis* occurring on the slopes and crests, usually in the gravelly loam, while *P. montanus* is limited to the clay of the lowland.

The flowers of these species are produced early and are short-lived, most of the foliage being produced after the flowers and continuing during the rainy vernal period, after which the surface parts disappear and the living parts lie buried until the following spring.

VERNAL ASPECT.

Habitat.—Physical water: in clay 13–17 per cent.; in gravelly loam 4.5–9 per cent. Non-available water: in clay 8.5–10 per cent.; in gravel 1.5–2.5 per cent. Available water: in clay 5.6–9.3^{gm} to 100^{gm} of dry soil; in gravel $3.2–7.2^{gm}$. Rainfall 12.7–27.9^{cm}; av. daily 0.3^{cm}. Relative humidity: mean 54 per cent.; range 11–100 per cent. Wind 5.33^{hm} per hour. Temperature: mean 14°.4 C.; mean max. 20°.5 C.; mean min. 6°.4 C.; range −2.2 −34°.4 C.; soil 12–25° C.; soil surface to 49° C. Light duration 67 per cent. Exposure varied, cover open, soil clay to gravel. Duration May 1 to July 15.

PRINCIPAL SPECIES: Senecio oblanceolatus Rydb., (Thelesperma intermedium Rydb.), Yucca glauca Nutt., Kellermannia yuccogena Ell. & Ev., Pleospora phragmospora Dur. & Mont., Astragalus Drummondii Dougl., Pentstemon angustifolius Pursh, P. secundiflorus Benth., (Opuntia polyacantha Haw.), (Carex stenophylla Wahl.), (Puccinia caracena DC.), Astragalus bisulcatus (Hook.) Gray, Euphorbia robusta (Engelm.) Small, Uromyces scutellatus (Schrank) Lév., Echinocereus viridiflorus Engelm., Arenaria Fendleri Gray, Sophora sericea Nutt., Uromyces hyalinus Pk., (Oreocarya suffruticosa [Torr.] Greene), (Ipomoea leptophylla Torr.).

SECONDARY SPECIES: Lesquerella montana (Gray) Wats., Tetraneuris glabriuscula Rydb., Aragallus Lambertii (Pursh) Greene, (Astragalus mollissimus Torr.), Astragalus crassicarpus Nutt., Lappula occidentalis (Wats.) Greene, Allium reticulatum Don, Oreocarya thyrsiflora Greene, Euphorbia glyptosperma Engelm., Hymenopappus cinereus Rydb., Thalesia fasciculata (Nutt.) Britton, Mertensia linearis Greene, Pentstemon Jamesii Benth., Eriogonum alatum Torr., Cactus viviparus Nutt., Malvastrum coccineum (Pursh) Gray, Cheiranthus arkansanus (Nutt.) Greene, Anogra coronopifolia (T. & G.) Britton, Gaura coccinea Pursh, Euphorbia serpyllifolia Pers., Tradescantia scopulorum Rose, Thelesperma gracile (Torr.) Gray, Astragalus Shortianus Nutt., Nothocalais cuspidata (Pursh) Greene, Erigeron pumilus Nutt., E. flagellaris Gray, E. glandulosus Porter, E. canus Gray, Carex filifolia Nutt., C. pennsylvanica Lam., Vicia americana Muhl., Aecidium porosum Pk., Quincula lobata (Torr.) Raf., Leucolene ericoides (Torr.) Greene, Meriolix serrulata (Nutt.) Walp., Lithospermum linearifolium Goldie, Anogra albicaulis (Pursh) Britton, Poa longipeduncula Scribn., Salvia lanceolata Willd., Gaura parviflora Dougl., Hedeoma nana (Torr.) Greene, Antennaria imbricata A. Nels., Evolvulus pilosus Nutt., Thelesperma intermedium Rydb., Sitanion elymoides (Torr.) Greene, Oreocarya suffruticosa (Torr.) Greene.

The vernal period, with which the prevernal is sometimes more or less blended, is ushered in by the spring rains and usually extends from about the first of May to the middle of July. The water content is higher at this period than any other, as is also the relative humidity. Extreme temperatures are not recorded, and the conditions for growth are more favorable than at any other time during the year.

This aspect is marked by the appearance of a great number of seedlings and by many showy flowering plants. The floral display is almost entirely of perennial plants. The earliest species generally appear on the north slopes or north crests, a position protected from the high temperature and excessive loss of water during the winter period.

Societies.

Senecio oblanceolatus society.—This society is by far the most important of the vernal period. It reaches its maximum development in the large gullies on the south side of the Mesa, but the species is distributed over practically the whole area.

Yucca glauca society (*fig. 7*).—This species is one of the most conspicuous plants of the Mesa region and in many places becomes dominant for this aspect. Since the plant is perennial, it is at all times one of the most characteristic of this part of the formation. Species of secondary importance in this society are *Senecio oblanceolatus*, *Euphorbia robusta*, *Lesquerella montana*, *Echinocereus viridiflorus*, and *Mertensia linearis*. This society is found on the gravelly soil, often on crests and slopes where the water content is especially low.

Pentstemon angustifolius society.—On crests in the south part of the Mesa this society reaches its best development. Here the species dominates areas of many square meters, almost to the exclusion of any other species. The chief secondary species of this society are *Lesquerella montana* and *Echinocereus viridiflorus*.

Euphorbia robusta society.—This society occurs on most of the hilltops and over rather large areas of the north Mesa. *E. robusta* is less dominant than the controlling species of the societies already mentioned. *Echinocereus viridiflorus* is in point of numbers more abundant but it is comparatively a very inconspicuous plant. *Senecio oblanceolatus* is not dominant in this society, but ranks second in importance to *Euphorbia robusta;* the society very naturally grading into the *Senecio oblanceolatus* society almost imperceptibly. Secondary species are *Lesquerella montana, Yucca glauca, Oreocarya thyrsiflora, Aragallus Lambertii, Mertensia linearis,* and *Erigeron pumilus.* The soil is a coarse, gravelly loam; water content 6–9 per cent.

FIG. 7.—Typical Mesa: Bouteloua formation; *Yucca glauca* society.

Arenaria Fendleri society.—On crests in coarse gravel or gravelly loam, where the water content is low, this society is found. *A. Fendleri* is dominant, but many other species help to make up the society. Among the more prominent secondary species are *Tetraneuris glabriuscula, Oreocarya thyrsiflora, Hymenopappus cinereus, Meriolix serrulata, Pentstemon angustifolius, Tradescantia scopulorum,* and *Lithospermum linearis.*

Pentstemon secundiflorus society.—No species of this aspect is more dominant than is *P. secundiflorus.* On the crests of the east and north sides of the Mesa it forms an extensive society. *Lesquerella montana, Echinocereus viridiflorus,* and *Evolvulus pilosus* are secondary species.

Astragalus bisulcatus society.—In the clay on the south, east, and west sides of the Mesa, large clumps of this species are very conspicuous at this time of the year. Its maximum development is at the bottom or near the bottom of the hillsides. It usually occurs alone, but we may also find it associated with *Sophora sericea, Quincula lobata, Lappula occidentalis, Allium reticulatum, Malvastrum coccineum,* and *Euphorbia glyptosperma.*

Astragalus Drummondii society.—This is an especially prominent society on north and west slopes, occupying about the same relative position as the *A. bisulcatus* society, but more extensive.

Sophora sericea society.—Although badly affected with *Uroymces hyalinus,* this species becomes the dominant plant in the clay draws of the south Mesa. The chief secondary species associated with it are *Lappula occidentalis, Allium reticulatum, Malvastrum coccineum,* and *Quincula lobata.*

Communities.

Among the secondary species are found a number which form communities. These are generally of limited extent, but are of species which are widely scattered throughout the formation. The following are the more important communities: *Tetraneuris glabriuscula,* on crests; *Lappula occidentalis,* in semiruderal situations; *Erigeron flageolaris,* at the base of north and west slopes, or on the north and west sides of clumps of oak which have entered from the foothill thicket formation; *E. glandulosus,* on north crests; *Carex filifolia,* on portions of the north Mesa and west slopes; *Quincula lobata,* in clay; *Opuntia polyacantha,* either in clay, or on the gravel crests; *Leucolene ericoides,* on south crests and slopes and other xerophytic situations; *Pentstemon Jamesii*, on clay knolls in the gullies of the south Mesa; *Malvastrum coccineum*, in semiruderal situations; *Gaura coccinea* and *Thelesperma gracile*, on open coarse gravel of north Mesa; *Poa longipeduncula*, on north slopes; *Salvia lanceolata*, in semiruderal situations; and *Antennaria imbricata*, on northwest and rarely northeast slopes.

Most of these communities are closed and contain very few if any other species belonging to this aspect. Any of the species which form societies will also be found to form communities; in fact some of the societies are merely associations of communities.

General.

The chief societies of the Mesa top are the *Yucca glauca* (*fig. 6*) and the *Senecio oblanceolatus* societies. These become more or less mixed in places on the north Mesa. In many places there is formed a mixed society which varies greatly and can only be regarded as a society made up by mixing the other societies and by the addition of widely distributed secondary species. The Mesa top contains besides the two prominent societies mentioned above, a society marked by *Euphorbia robusta*. These three societies alternate, the last named occurring on the north part, the more open part of the formation, in gravelly loam, where the water content is from 6–10 per cent. The *Yucca glauca* society occupies a somewhat more humid region—the crests and Mesa top, especially where the soil is a rocky, gravelly loam, with water content from 7–12 per cent. The *Senecio oblanceolatus* society reaches its maximum development in the gullies, where the loam has a water content of 10–15 per cent.

In addition to these well-marked societies, the following plants occur in varying numbers over practically the whole Mesa top: *Lesquerella montana*, *Pentstemon angustifolius*, *Aragallus Lambertii*, *Astragalus crassicarpus*, *Oreocarya thyrsiflora*, *Erigeron pumilus*, *E. canus*, *Astragalus Shortianus*, and *Mertensia linearis*. Any or all of these species may occur in the societies noted above.

The gravel crests with a water content of from 4.5–9 per cent. are the most xerophytic situations in the formation; and here are found several societies that alternate. Most of the crests of the north and east sides of the Mesa are occupied by the *Pentstemon* *secundiflorus* society; the crests of the south Mesa by the *P. angustifolius* society; and the west crests in either situation or on the west side by the *Arenaria Fendleri* society. The alternation between the first two societies is very marked and may be explained partly by the facts of development. *P. secundiflorus* occurs on soil that is less disintegrated, on coarse gravel, or coarse gravelly loam. *P. angustifolius* occurs in older gravelly loam, where the water content is from 2–4 per cent higher; it seems to be more at home on the plains, while *P. secundiflorus* thrives best in the foothill region. These societies also alternate with the *Arenaria Fendleri* society.

There are in this aspect no well-developed societies on the hillsides. The flora of the slopes however, is rather rich and varied. Practically all of the societies are represented here and one may also find many of the secondary species. Crest forms are especially abundant on the south and east slopes.

The alternation between the *Astragalus bisulcatus* society and the *A. Drummondii* society is partly due to the difference in soil. *A. bisulcatus* occurs in clay and is best developed on south and west exposures, usually at the base of the hills. North and west exposures are the most suitable for *A. Drummondii*, which likewise occurs at the base of the hills.

On the lower land surrounding the Mesa the flora is largely of the *Astragalus bisulcatus* society and of the *Sophora sericea* society, together with the following communities: *Lappula occidentalis*, *Quincula lobata*, *Opuntia polyacantha*, *Malvastrum coccineum*, and *Salvia lanceolata*. This vegetation is in the Ft. Pierre clay, a heavy soil with a water content of 13–17 per cent., 8–10 per cent. of which is not available.

As seen by this arrangement, there is zonation exhibited by these societies. This, however, is not very well marked, and the alternation within the zones is much more distinct than the zones themselves.

The reason for this alternation within the formation is to be found in the physical nature of the soil. The soil of the Mesa is a gravel, mixed with a limited amount of humus and silt, or even clay, and is derived entirely from partly decomposed granite and plant remains. The soil is pervious and there is consequently very little run-off, except during very heavy rains. The total water content varies with the soil composition from 5–14 per cent., and all but 2–4 per cent. is available to the plant. The crests are of a much looser soil, almost pure gravel in places, but generally mixed with clay and silt. The water content here is from 3–4 per cent. lower than on the Mesa top and the formation is much more open. The clay is closely packed and a large percentage of water which falls runs off. The water content is usually less than 17 per cent. and is often as low as 13 per cent., while the non-available water seems to vary with the plant and the slight differences in the amount of foreign substances in the clay from 8.5–10 per cent. After a rain the soil is easily baked to form a hard crust, and when the soil becomes dry, especially during winter, it cracks open to a considerable depth.

The preference which certain plants show for north and west slopes is easily explained by a glance at the sunshine record for June and July. The morning sun heats the east slopes, and as it rises higher the south slope is strongly heated. This hastens transpiration and water loss. The afternoon is cloudy and very likely rainy. The west slope is consequently not strongly illuminated, the soil temperature is from 2–5° C. lower than on the east and south slopes, and the water content is from 1.5–5 per cent. higher. It is the least xerophytic of any situation in the formation.

AESTIVAL ASPECT.

Habitat.—Physical water: in clay 10–13 per cent.; in gravel 2.5–4.5 per cent. Non-available water: in clay 8.5–10 per cent.; in gravel 1.5–2.5 per cent. Available water: in clay 2.3–3.8^{gm} to 100^{gm} of dry soil; in gravel 1–2.1^{gm} to 100^{gm}. Rainfall 7.59–10^{cm}; av. daily 0.137^{cm}. Relative humidity: mean 51 per cent.; range 9–100 per cent. Wind 4.354^{hm} per hour. Temperature: mean 18.8° C.; mean max. 25° C.; mean min. 10.5° C.; range 2.7°–36.6° C.; soil 18–29° C.; soil surface to 55° C. Light duration 55 per cent. Exposure varied, cover open, soil clay to gravel. Duration July 15 to September 15.

FACIES: Bouteloua oligostachya (Nutt.) Torr., B. hirsuta Lag., (Andropogon scoparius Mich.), (A. furcatus Muhl.), (Calamovilfa longifolia [Hook.] Hack.), Muhlenbergia gracillima Torr., Agropyrum occidentale Scrib., (Koeleria cristata [L.] Pers.).

PRINCIPAL SPECIES: Artemisia frigida Willd., (Thelesperma intermedium Rydb.), (Schedonnardus paniculatus [Nutt.] Trel.), Gutierrezia Sarothrae (Pursh) Britt. & Rusby, (Grindelia squarrosa [Pursh] Dunal), Chrysopsis villosa (Pursh) Nutt., (Eriogonum annuum Nutt.), (Artemisia canadensis Michx.), Lupinus argenteus Pursh), (Carduus plattensis Rydb.), Aristida longiseta Steud., Psoralea tenuiflora Pursh., Aecidium psoralea Pk., Boebera papposa (Vent.) Rydb., Plantago Purshii R. & S., (Selaginella densa Rydb.), (Eriogonum effusum Nutt.), (Sporobolus cryptandrus [Torr.] Gray), (Eriogonum annuum Nutt.)

SECONDARY SPECIES: Oreocarya thyrsiflora Greene, Petalostemon oligophyllus (Torr.) Rydb., P. purpureus (Vent.) Rydb., Euphorbia glyptosperma Engelm., Thelesperma gracile (Torr.) Gray, Gaura coccinea Pursh, Tetraneuris glabriuscula Rydb., Malvastrum coccineum (Pursh) Gray, Atheropogon curtipendulus (Michx.) Fourn., Sideranthus spinulosus (Nutt.) Sweet, Laciniaria punctata (Hook.) Kuntze, Eriogonum Jamesii Benth., Munroa squarrosa (Nutt.) Torr., Euphorbia serpyllifolia Pers., Chenopodium leptophyllum (Moq.) Nutt., Mentzelia nuda (Pursh) Torr. & Gray, Argemone intermedia Sweet, Physalis comata Rydb., Atriplex argentea Nutt., Potentilla pennsylvanica L., Asclepias pumila (Gray) Vail, Bouteloua prostrata Lag., Helianthus pumilus Nutt., Sitanion elymoides Raf., Muhlenbergia gracilis Trin., Artemisia gnaphalodes Nutt., Stipa comata Trin. & Rupr., Stipa Vaseyi Scrib., Allionia linearis Pursh, Artemisia canadensis Michx., Leucolene ericoides (Torr.) Greene, Picradeniopsis oppositifolia (Nutt.) Rydb., Hedeoma nana (Torr.) Greene, Stipa neo-mexicana (Thurb.) Scrib., Chenopodium oblongifolium Wats., Anogra coronopifolia (T. & G.) Britton, Leptilon canadense (L.) Britton, Helianthus annuus L., Andropogon furcatus Muhl., Solanum rostratum Dunal, Ptiloria ramosa Rydb., Chenopodium album L., Helianthus petiolaris Nutt., Quincula lobata (Torr.) Raf., Grindelia squarrosa nuda (Wood) Gray, Carduus undulatus Nutt., Carduus plattensis Rydb., Gaura parviflora Dougl., Potentilla coloradensis Rydb., Eriogonum alatum Torr., Euphorbia stictospora Engelm., Mentzelia decapetala (Pursh) Urban & Gilg, Andropogon scoparius Michx.

An increase in temperature, a decrease in rainfall and relative humidity, together with the resulting decrease in water content of the soil mark the appearance of the aestival period. The percentage of water in the soil is for this period 10–13 per cent. for clay and 2.5–4.5 per cent. for gravel.

This aspect is characterized by the flowering of most of the annual species and by the predominance of the grasses and composites. The facies of the formation are the dominant species of this aspect and in consequence the principal species are less conspicuous than during the vernal period.

Consocies.

Consocies or areas dominated by the facies of the formation will be discussed later, and need only be mentioned here.

Bouteloua oligostachya consocies.—This consocies is almost as extensive as is the formation, for this species is by far the most abundant of any found in the region studied. A discussion of the consocies is practically a discussion of the typical grama grass formation and will be taken up later. The highest development of this consocies is on the Mesa top, where the water content of this period in the gravelly loam is 4–8 per cent.

Bouteloua hirsuta consocies.—This consocies occupies a more xerophytic habitat, where the water content is 2.5–4.5 per cent. It occurs on the crests and on the north portion of the Mesa in the gravelly soil. With this plant are generally associated *Artemisia frigida, Atheropogon curtipendulus, Aristida longiseta, Bouteloua oligostachya, Gutierrezia Sarothrae,* and many crest species. Conditions here are the most xerophytic of any situation in the habitat.

Muhlenbergia gracillima consocies.—This consocies is characteristic of the clay flats where it reaches its best development. It is not uncommon to find places which are dominated by this species almost to the exclusion of everything else. As a rule, however, one finds here *Bouteloua oligostachya, Schedonnardus paniculatus, Artemisia frigida, Gutierrezia Sarothrae, Munroa squarrosa, Boebera papposa, Plantago Purshii, Picradeniopsis oppositifolia, Euphorbia glyptosperma, Argemone intermedia, Atriplex argentea, Agropyron occidentale, Malvastrum coccineum,* and many other secondary species. The habitat is xerophytic, in clay or loam where the water content varies with the soil composition from 17–13 per cent.; the available water being from 2–3.5^{gm} per 100^{gm} of dry soil.

Agropyron occidentale consocies.—This is not so important in the Mesa region as it is farther east. It occurs, however, in the clay, and here is usually associated with *Muhlenbergia gracillima, Bouteloua oligostachya, B. prostrata,* and *Atriplex argentea.*

Societies.

Artemisia frigida society.—This is by far the most important society of the region. It occurs at the heads of the gullies and on the more depressed places of the north Mesa. It is also important on alluvial fans and areas where there has been a secondary succession. Where this species is abundant, as a rule it shuts out all other plants with the exception of the taller species, such as *Argemone intermedia* and *Stipa Vaseyi.* This society can be distinguished for miles because of the silvery appearance of the plant, which is so widely distributed over the entire Mesa that it would be considered a facies of the formation if it were not for the fact that more extended study shows it to be local in its distribution.

Gutierrezia Sarothrae society.—This composite is rather evenly distributed over the Mesa region, but it can never be said to replace the grasses which are characteristic of the formation. It does dominate rather large areas, however, particularly in the southern part of the Mesa, where it is found associated with many of the characteristic plants of the Mesa top. It does not occur so commonly in the purer gravel soil as in the clay and gravelly loam.

Chrysopsis villosa society.—This society is of considerable importance on the north portion of the Mesa, where it occurs in the *Bouteloua hirsuta* consocies.

The *Aristida longiseta* society is not extensive, but dominates south and east crests and slopes. The *Psoralea tenuiflora* society is extensive, reaching its best development on the hillsides.

The rainy vernal period favors the development of a number of annuals which come into bloom at this time. The most important of these is *Boebera papposa,* which has a very even distribution throughout the region studied. It occurs as a ruderal plant, usually from 4–10^{cm} high and bearing very often only one head. In point of numbers it probably exceeds all but the facies of the formation. However, it succeeds best as a ruderal, and in the formation the small plants may be as numerous as 996 per quadrat and still not be especially noticeable. Wherever there are open spaces in the formation, this society is found.

Plantago Purshii also occurs as an important annual in the formation. It is also successful as a ruderal, but at places within the formation may become far more numerous than any other species.

Communities.

The following communities also occur: *Schedonnardus paniculatus*, near the mountain and in clay; *Atheropogon curtipendulus*, on north slopes; *Sideranthus spinulosus*, on south slopes and crests; *Atriplex argentea*, in ruderal clay; *Bouteloua prostrata*, in clay south of the Mesa, also in ruderal or semiruderal habitats; *Sitanion elymoides*, on south slopes; *Muhlenbergia gracilis*, on north slopes; *Artemisia canadensis*, on north and west slopes; *Leucolene ericoides*, crests and xerophytic places; *Andropogon furcatus*, on north Mesa in gravel; *Andropogon scoparius*, on gravel crests; *Thelesperma gracile* and *Gaura coccinea* continue from the previous aspect.

Within this area there is one family of *Oonopsis foliosa* (Gray) Greene, which is about three years old and has spread to occupy 25^{sqm}.

General.

In considering the aestival aspect as a whole, much is found that will be discussed under the formation. Zonation during this aspect is shown as in the preceding aspect. The Mesa top is dominated by the typical formation—*Bouteloua oligostachya* consocies—the crests by the *B. hirsuta* consocies, the hillsides by the typical formation tending towards the *B. hirsuta* consocies, and the low lands surrounding either by the typical formation or by this alternating with the *Muhlenbergia gracillima* or *Andropogon occidentale* consocies.

This zonation is largely due to differences in water content. The Mesa top and the slopes have nearly the same water content, there being about $2\text{–}3^{\mathrm{gm}}$ of available water; the crests have a less amount, $1\text{–}2^{\mathrm{gm}}$; while at the base, in the clay, the available water is from $2.3\text{–}3.8^{\mathrm{gm}}$.

The greater part of the Mesa top is occupied by the *Bouteloua oligostachya* consocies. Almost any of the other species noted under this aspect, whether they are primary or secondary, may be found associated with *B. oligostachya*. The most noticeable forms found on the Mesa at this time are *B. oligostachya*, *Muhlenbergia* *gracillima*, *Bouteloua hirsuta*, *Artemisia frigida*, *Gutierrezia Sarothrae*, *Boebera papposa*, *Oreocarya thyrsiflora*, *Chrysopsis villosa*, *Schedonnardus paniculatus*, *Petalostemon oligophyllus*, *P. purpureus*, *Psoralea tenuiflora*, *Thelesperma gracile*, *Gaura coccinea*, *Euphorbia glyptosperma*, *Atheropogon curtipendulus*, *Sideranthus spinulosus*, *Lacinaria punctata*, *Eriogonum Jamesii*, *E. effusum*, *Asclepias pumila*, *Helianthus pumilus*, *Sitanion elymoides*, *Artemisia gnaphalodes*, *Castilleia integra*, *Erigonum alatum*, *Pentstemon unilateralis*, *Stipa Vaseyi*, and *Euphorbia stictospora.*

Besides the typical formation, the north Mesa is occupied by the *Bouteloua hirsuta* consocies. In this consocies the following groups occur: the *Chrysopsis villosa* society occupying rather limited areas, low crests, and south slopes; and the following communities: *Sideranthus spinulosus*, *Artemisia gnaphalodes*, *Andropogon furcatus*, and *A. scoparius.*

The crests are the most xerophytic and are occupied by the *Bouteloua hirsuta* consocies. This may alternate, however, with the *B. oligostachya* consocies. Occurring within the former consocies are often found the *Gutierrezia Sarothae*, *Chrysopsis villosa*, and the *Aristida longiseta* societies, as well as the following communities: *Sitanion elymoides*, *Muhlenbergia gracilis*, *Artemisia gnaphalodes*, *Andropogon scoparius*, and *Tetraneuris glabriuscula.* The following plants are also abundant on these crests: *Oreocarya thyrsiflora*, *Chenopodium leptophyllum*, *Stipa comata*, and *S. neo-mexicana.*

The hillsides and slopes have usually about the same vegetation as the Mesa top, but the crest forms may be more abundant.

Passing to the lowlands, the *Bouteloua oligostachya* consocies is found alternating with the *Muhlenbergia gracillima* consocies and also the *Andropogon occidentale* consocies. The chief societies of the *Bouteloua oligostachya* consocies are the *Gutierrezia Sarothrae* and *Artemisia frigida* societies. In the Muhlenbergia consocies are found the *Bouteloua prostrata* and *Atriplex argentea* communities.

Marked alternations sometimes occur between secondary species. *Petalostemon oligophyllus* occurs on south and east slopes, and *P. purpureus* on north and west slopes, where the water content is from 1–2 per cent. higher; *Muhlenbergia gracile*, *Koeleria cristata*, and *Potentilla pennsylvanica* are usually found on north slopes;

while *Aristida longiseta, Sitanion elymoides, Stipa comata, S. neomexicana, Physalis comata,* and *Ptilora ramosa* are found on south slopes and crests.

AUTUMNAL ASPECT.

Habitat.—Physical water: in clay 8.5–10 per cent.; in gravel 1.5–2.5 per cent. Non-available water: in clay 8.5–10 per cent.; in gravel 1.5–2.5 per cent. Available water: none in surface soil. Rainfall 1.62–4.03^{cm}; av. daily .006^{cm}. Relative humidity: mean 49 per cent.; range 12–100 per cent. Wind 4.66^{hm} per hour. Temperature: mean 11.6°C.; mean max. 18.8°C.; mean min. 2.7°C.; range −5.5°−27.2°C.; soil 18–25°C.; soil surface to 40°C. Light duration 60 per cent. Exposure varied, cover open, soil clay to gravel. Duration September 15 to November 1.

PRINCIPAL SPECIES: Artemisia frigida Willd., Gutierrezia Sarothrae (Pursh) Britt. & Rusby, (Grindelia squarrosa [Pursh] Dunal), Senecio spartioides Torr. & Gray, Chrysopsis villosa (Pursh) Nutt., Chrysothamnus graveolens (Nutt.) Greene.

SECONDARY SPECIES: Lacinaria punctata (Hook.) Kuntze, Oreocarya thyrsifloria Greene, Eriogonum Jamesii Benth., Aster polycephalus Rydb., Machaeranthera cichoriacea Greene, Tetraneuris glabriuscula Rydb., Munroa squarrosa (Nutt.) Torr., Petalostemon purpureus (Vent.) Rydb., P. oligophyllus (Torr.) Rydb., Artemisia canadensis Michx., A. gnaphalodes Nutt., Grindelia squarrosa (Pursh) Dunal, Leptilon canadense (L.) Britton, Machaeranthera viscosa Nutt., Chrysothamnus plattensis Greene, Grindelia squarrosa nuda (Wood) Gray, Eurotia lanata (Pursh) Moq.

During the month of August the rainfall decreases markedly, and is only slight during September. The temperature at this time is as high as at any time during the year, and the result is the rapid loss of water by the soil. Although there is still 8–10 per cent. of water in clay and 1.5–2.5 per cent. in gravel, it is doubtful if there is any available water in the surface soil.

Although many plants continue to bloom, vegetative growth is practically stopped for all annuals and greatly decreased for perennials. There must still be some available water, but all the annual plants which would ordinarily continue to grow and bloom if supplied with only a limited amount of water, have dried up at the beginning of this period. The grasses are dried, and although they are still a prominent part of the vegetation, they are not a living part. It is an exceedingly xerophytic time, and the plants which are found in this aspect appear throughout the vernal and aestival periods and are now only blooming and ripening their seeds.

Artemisia frigida and *Muhlenbergia gracillima* continue to occupy a most important place. *Senecio spartioides* forms in places an extensive society; while the *Gutierrezia Sarothrae* society is even more noticeable than during the aestival period. *Chrysothamnus graveolens*, a large shrubby composite, forms a small society within this region, but farther east occupies larger areas; it is one of the most showy plants of this aspect. *Aster polycephalus* and *Machaeranthera cichoriacea* form rather extensive communities in the more open parts of the formation. *Chrysopsis villosa, Lacinaria punctata, Oreocarya thyrsiflora, Eriogonum Jamesii, Tetraneuris glabriuscula, Petalostemon oligophyllus, P. purpureus, Aristida longiseta, Grindelia squarrosa, G. squarrosa nuda, Artemisia canadensis,* and *A. gnaphalodes* have continued from the preceding period.

The end of this period is not well marked. The plants are dry and resistant, and although frost kills the plants which have a more liberal supply of water, some of these species may continue to bloom as late as December 10. During this late period *Senecio oblanceolatus, Argemone intermedia, Lesquerella montana,* and a number of other species form rosettes which continue throughout the winter.

Structure of the formation as illustrated by typical quadrats.

Passing now from the aspects to the formation as a whole, the structure may be illustrated best by a number of permanent quadrats. Those species which form mats cannot be well represented in numbers per square meter, and on this account the percentage of surface covered is given instead. The numbers which are also given for these species indicate single plants or seedlings. An estimate is also given of the total amount of surface covered by plant growth.

The following quadrat is typical of the *Bouteloua oligostachya* consocies—the most typical portion of the Bouteloua formation.

Bouteloua oligostachya	134	22%	Senecio spartioides	4
Muhlenbergia gracillima	5	7%	Sideranthus spinulosus	12
Artemisia frigida	6	5%	Boebera papposa	81
Senecio oblanceolatus	9		Plantago Purshii	2
Aristida longiseta	1		Polygonum aviculare	1
Astragalus Shortianus	1		Townsendia exscapa	1
Schedonnardus paniculatus	1		Bryum argenteum	
Chrysopsis villosa	1		Total surface covered	42%

Water content: vernal period 8–13%; aestival 6–8%; autumnal 5–6%. Soil, gravelly loam.

The most important difference in the habitat is in water content, the other factors being practically the same as given under the aspects of the formation.

The following quadrats are also typical of the *Bouteloua oligostachya* consocies, but represent this consocies as modified by the occurrence within it of societies.

Bouteloua oligostachya	47%	Euphorbia stictospora	9
Artemisia frigida	4.5%	Boebera papposa	996
Anogra coronopifolia	21	Anogra albicaulis	2
Senecio oblanceolatus	1	Total surface covered	56%

Water content: vernal period 6–12%; aestival 46%; autumnal 3–4%. Soil, fine gravelly loam.

A quadrat within a *Gutierrezia Sarothrae* society:

Bouteloua oligostachya	168	Eriogonum effusum	5
Gutierrezia Sarothrae	22	Boebera papposa	5
Artemisia frigida	10	Malvastrum coccineum	6
Sideranthus spinulosus	18		

Water content: vernal period 7–15%; aestival 4–7%; autumnal 2–4%. Soil, coarse gravelly loam mixed with lime.

The following quadrat will serve to illustrate a portion intermediate between the *Bouteloua oligostachya* consocies and the *Muhlenbergia gracillima* consocies.

Muhlenbergia gracillima	20	33%	Boebera papposa	36
Bouteloua oligostachya	24	12%	Atheropogon curtipendulus	1
Sideranthus spinulosus	3		Allionia linearis	1
Malvastrum coccineum	5		Echinocereus viridiflorus	1
Artemisia frigida	2		Total surface covered	47%

Water content: vernal period 8–14%; aestival 6–8%; autumnal 5–6%. Soil, loam.

Muhlenbergia gracillima consocies.—This consocies covers the greater part of the lower land, particularly that south of the Mesa. The following quadrat is typical.

Muhlenbergia gracillima		46%	Boebera papposa	25
Schedonnardus paniculatus		6%	Plantago Purshii	9
Bouteloua oligostachya		1%	Senecio oblanceolatus	1
Artemisia frigida	19	1.5%	Hedeoma nana	1
Munroa squarrosa	1		Salvia lanceolata	1
Gutierrezia Sarothrae	9		Euphorbia glyptosperma	1
Picradeniopsis oppositifolia	3		Total surface covered	56%

Water content: vernal period 9–14%; aestival 7–9%; autumnal 5–7%. Soil, loam.

This consocies should also show *Opuntia polyacantha, Stipa Vaseyi, Argemone intermedia, Senecio spartioides, Verbena bracteosa, Atriplex argentea, Malvastrum coccineum, Astragalus crassicarpus, A. bisulcatus, Sophora sericea, Quinculata lobata, Agropyron occidentale,* and many others.

In places *Muhlenbergia gracillima* is even more dominant than in the quadrat given above, but as one passes to the higher ground it gives way gradually to *Bouteloua oligostachya.*

Bouteloua hirsuta consocies.—This consocies is best developed on the crests and over the north portion of the Mesa. A quadrat best illustrates the structure.

Bouteloua hirsuta	95	17%	Sideranthus spinulosus	7
Artemisia frigida		4%	Oreocarya thyrsiflora	6
Atheropogon curtipendulus		1.5%	Lacinaria punctata	4
Aristida longiseta	4	1%	Gaura coccinea	3
Andropogon scoparius		.5%	Euphorbia robusta	2
Bouteloua oligostachya		.3%	Senecio spartioides	1
Thelesperma gracile	16		Astragalus Shortianus	1
Echinocereus viridiflorus	8		Pentstemon secundiflorus	1
Senecio oblanceolatus	7		Total surface covered	32%

Water content: vernal period 4.5–9%; aestival 2.5–4.5%; autumnal 1.5–2.5%. Soil, coarse gravelly loam. This quadrat also illustrates the structure of the vernal *Euphorbia robusta* society.

While *Bouteloua hirsuta* is predominant in this consocies, many other species are important. *Muhlenbergia gracillima* is sometimes present; *Aristida longiseta* and *Sitanion elymoides* are sometimes very important; *Andropogon furcatus*, *Yucca glauca*, *Erigeron pumilus*, and *E. canus* are often present.

The physical conditions of this consocies are not essentially different from those of the typical formation, except that the looser, gravelly soil contains less water. It is the most xerophytic of all the consocies. The following crest quadrat from the south part of the Mesa also illustrates this consocies.

Bouteloua hirsuta	35	10%	Artemisia frigida	2
Bouteloua oligostachya	34	3%	Senecio oblanceolatus	2
Aristida longiseta	8	1.5%	Gaura coccinea	1
Atheropogon curtipendulus	30	.5%	Oreocarya thyrsiflora	1
Gutierrezia Sarothrae	7		Echinocereus viridiflorus	1
Senecio spartioides	3		Lecanora subfusca allophana*	20
Pentstemon angustifolius	3		Total surface covered	23%

* Small crusts—a remnant of the more primitive lichen formation.

Water content: vernal period 6–10%; aestival 4–6%; autumnal 2.5–4%. Soil, very coarse gravelly loam.

Societies of the *Bouteloua hirsuta* consocies: *Pentstemon secundiflorus* society found on crests of the north or east part of the Mesa. The following quadrat is typical:

Pentstemon secundiflorus, (81 in bloom)	141		Evolvulus pilosa	7
Artemisia frigida		7%	Sideranthus spinulosus	6
Bouteloua hirsuta	65		Echinocereus viridiflorus	2
Lesquerella montana (seedlings)	40		Mentzelia nuda	4
Boebera papposa	8		Portulaca oleracea	1
			Total surface covered	24%

Water content: vernal period 4.5–9%; aestival 2.5–4.5%; autumnal 1.5–2.5%. Soil, coarse gravelly loam.

Pentstemon angustifolius society.—While *Pentstemon angustifolius* does not form so dense an association as *P. secundiflorus*, the spikes are much larger, and it is therefore very prominent in certain areas. The following quadrat is typical:

Bouteloua hirsuta	17	20%	Artemisia canadensis	2
Pentstemon angustifolius	14	(5%)	Eriogonum Jamesii	1
Aristida longiseta		1%	Thelesperma gracile	1
Chrysopsis villosa	8		Boebera papposa	4
Allionia linearis	5		Euphorbia stictospora	4
Echinocereus viridiflorus	2		Total surface covered	28%
Gutierrezia Sarothrae	2			

Water content: vernal period, 6–12%; aestival 4–6%; autumnal 2–4%. Soil, coarse gravelly loam.

This society belongs to the vernal aspect and alternates markedly with the above-mentioned society. So distinct is this alternation, that on adjacent crests these societies may occur with no mixing of the dominant species. It occupies the south and west crests of the Mesa. The species is widely distributed over the top of the Mesa, but seldom becomes dominant.

The following quadrat is taken from a community of *Leucolene ericoides:*

Leucolene ericoides	78	Eriogonum Jamesii	1
Bouteloua hirsuta	53	Psoralea tenuiflora	1
Aristida longiseta	13	Allionia linearis	1
Eriogonum effusum	3	Chenopodium leptophyllum	1

The *Agropyron occidentale* consocies is not as well developed in this region as elsewhere, but the following quadrat will show the structure. This quadrat is taken from a community of *Bouteloua prostata.*

Bouteloua prostrata	352	Salvia lanceolata	11
Agropyron occidentale	216	Polygonum aviculare	10
Bouteloua oligostachya	47	Picradeniopsis oppositifolia	9
Boebera papposa	123	Quincula lobata	4
Verbesina encelioides	108	Salsola Tragus	2
Gutierrezia Sarothrae	23		

Water content: vernal period 13–17%; aestival 10–13%; autumnal 8.5–10%. Soil, clay.

General discussion.

While the vegetation of the Mesa is typical of the high plains, it does not show all of the structure that is at once apparent upon the examination of a larger area. On the Great Plains lying east, this formation is everywhere in evidence. By far the most important species is *Bouteloua oligostachya*—the dominant species of the formation. That part of the formation which is most typical is the *B. oligostachya* consocies. This consocies is much more closed and pure on the great level plateau farther east than it is near the mountains. It often covers as much as 60–70 per cent. of the surface, and is associated with very few primary or secondary species. In the clay flats it often gives way to the *Muhlenbergia gracillima* or *Agropyron occidentale* consocies, and in passing to sandy or gravelly ridges it is often dominated by the *Bouteloua hirsuta*, *Andropogon scoparius*, or *Koeleria cristata* consocies. Even on the slopes or more level sandy areas it alternates with the *Calamovilfa longifolia* consocies, and at times with the *Andropogon furcatus* consocies. Although these consocies dominate immense areas, they are not to be regarded as constituting distinct formations. *Bouteloua oligostacyha* is prominent everywhere and these are merely modifications of the Bouteloua formation, or in other words, consocies of this formation.

To discuss each aspect of this formation would take too much space, and some idea may be obtained by referring to the lists given earlier in this paper.

There is a rather marked zonation in regions characterized by rolling or uneven ground. The hills and ridges are occupied by *Bouteloua hirsuta*. In this habitat there is a rather marked alternation with other consocies. *Andropogon scoparius* often becomes dominant, as does also *Koeleria cristata*. Here are also found a number of prominent societies, among which the most xerophytic is the *Selaginella densa* society. *Sporobulus cryptandrus* and *Stipa comata* may also become prominent.

Occupying the sides of the slopes and the level expanses is the extensive *Bouteloua oligostachya* consocies. Alternating with this is found the *Andropogon furcatus* and the *Calamovilfa longifolia* consocies. This alternation is often very marked, the consocies remaining distinct from each other.

It is here that the most important societies of the formation are found, many of which extend for many miles without interruption. Among the most prominent of these societies is the *Grindelia squarrosa* society, which extends for many miles east of Limon, Col., and occurs over less extensive areas in many other parts of the formation. The *Schedonnardus paniculatus* society occurs throughout the formation and in many places is very extensive. Between Burlington, Col., and Goodland, Kans., the society extends for many miles. *Thelesperma intermedium* also occurs in this consocies. It is one of the most prominent societies in the formation and is especially well developed just east of Colorado Springs. The *Gutierrezia Sarothrae* society occurs more often near the mountains and bluffs. *Artemisia canadensis* is also important in similar locations, while *A. dracunculoides* is most abundant farther out on the plains. *Opuntia polyacantha* in most places merely forms small communities or families, but in many places on the plains these become associated into an extensive society. This is especially true east and south of Fountain, Col. *O. arborescens* is also found in this region and extends northward to within a few miles of Colorado Springs.

Carex stenophylla, *Senecio oblanceolatus*, *Sophora sericea*, *Astragalus Drummondii*, *Oreocarya suffruticosa*, *Eriogonum annuum*, *Chrysopsis villosa*, *Boebera papposa*, and *Plantago Purshii* each form extensive societies in this consocies. The following societies are not so extensive, but on account of the prominence of the plants characterizing them they are very noticeable: *Ipomoea leptophylla*, *Yucca glauca*, *Lupinus argenteus*, *Carduus plattensis*, *Eriogonum effusum*, *Chrysothamnus graveolens*, *Senecio spartioides*, *Pentstemon angustifolius*, *P. secundiflorus*, and *Astragalus bisulcatus*.

Passing now to the lowlands, the *Bouteloua oligostachya* consocies is found with very few primary or secondary species, and usually alternating with the *Muhlenbergia gracillima* and the *Agropyron occidentale* consocies. These consocies are sometimes mixed, but as a rule remain distinct. *Agropyron occidentale*, a tall slender grass, is usually not associated with many other species, and the mats of *Muhlenbergia gracillima* also leave little space for the development of any but a few of the clay-loving annuals. *Astragalus bisulcatus*, *Sophora sericea*, *Boebera papposa*, *Plantago Purshii*, and *Atriplex argentea* are among the most important secondary species of these consocies.

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CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. VII.

Aven Nelson.

Cypripedium Knightae, n. sp.—Stem short, $3–7^{\mathrm{cm}}$ high, sparsely and coarsely villous, bearing a single pair of nearly opposite leaves at its summit: leaves oval, generally rounded and obtuse, thickish $4–7^{\mathrm{cm}}$ long: peduncle glandular-viscid, $3–10^{\mathrm{cm}}$ long, usually naked rarely with a lanceolate bract near the middle: floral bracts rather large, elliptic-lanceolate: flowers 2 or 3 in a cluster, dark-purple: lower sepals united nearly to the tip, ovate-lanceolate, the two together no broader than the other sepal: petals similar, a little broader than the sepals: lip $10–12^{\mathrm{mm}}$ long, somewhat shorter than the sepals and petals, the deeply infolded free margin deep-purple, the lower part of the sac ochroleucous or greenish-yellow: sterile anther elliptic, obtuse, much shorter and smaller than the large conspicuous stigma.

This species, in so far as it has been collected, has seemingly passed as *C. fasciculatum* Kellogg, Wats. Proc. Am. Acad. 17:380. That is a very different thing, as may be seen by referring to the original description, or to Howells's Fl. N. W. Am. 632. It is, moreover, of a quite different geographical range. I have great pleasure in naming this fine species for Miss Harriet Knight, whose sympathetic interest in all nature and whose intelligent activity in the educational work of Wyoming is greatly appreciated.

Collections at hand: *Miss Knight*, Medicine Bow Mts., Wyo., at Cooper Hill, July 1905 (type); *L. N. Goodding*, no. 1201, Uinta Mts., Utah (Dyer Mine), June 30, 1902; *G. E. Osterhout*, Estes Park, Colo., July 1897; and Encampment Creek, Sept. 1897.

Montia Viae, n. sp.—Annual, with fibrous roots: stems and petioles weak, suberect, $10–15^{\mathrm{cm}}$ high: leaves delicately thin, pale-green; the radical several, slender-petioled, the short blades from linear to oval, acute; the single pair of cauline connate and forming a circular or slightly irregular involucral disk $10–20^{\mathrm{mm}}$ broad: raceme peduncled, with a pair of green bracts at the base of the lower pedicels: flowers very small, several: sepals broadly oval, even in fruit less than 2^{mm} long: petals 5, spatulate, barely equalling the sepals, very delicate, apparently often wholly wanting: stamens 5, very short: ovule solitary; the seed small, oval, slightly compressed and subcarinate, minutely but distinctly papillose-roughened and with a waxy conspicuous strophiole.

Most nearly related but very distinct from *M. perfoliata* (Donn.) Howell, Erythea 1:38, a plant of the Pacific states. Possibly all of the central Rocky Mountain specimens named *M. perfoliata* belong here. The type specimens were collected by the Misses *Dorothy Reed* and *Vie Willits*, June, 1905. Miss Willits, in whose honor the plant is named, later secured an abundance of fruiting specimens. Type locality, shady muddy banks, Big Horn, Sheridan Co., Wyoming.

Lesquerella latifolia, n. sp.—Perennial, silvered with a fine lepidote stellate pubescence throughout: stems numerous, from among the crowded rosulate crown leaves, decumbent at base, spreading, 5–15^{cm} long: radical leaves suborbicular, oval, or rhombic, sometimes broader than long, from 1–3^{cm} in diameter; the petioles slender, often much longer than the blade; cauline leaves from broadly obovate to spatulate, all cuneately tapering into a slender petiole: racemes of showy bright-yellow flowers dense, elongating in fruit: petals spatulate, 9–10^{mm} long, twice as long as the oblong sepals: siliques elliptic, very perceptibly stipitate, 5–6^{mm} long, erect on S-shaped pedicels of about the same length; style slender, 3–4^{mm} long; cells about 5-ovuled.

This is based upon Mr. L. N. Goodding's no. 625, from Karshaw, Meadow Valley Wash, southern Nevada, Apr. 26, 1902. It has been distributed as *L. montana*, a species from which it is as far removed as to characters as it is geographically.

Lesquerella Lunellii, n. sp.—Pale green, moderately and minutely stellate-pubescent throughout: caudex a mere crown surmounting the slender tap root: stems few to several, ascending or assurgent, very slender (almost filiform), 3–15^{cm} long (including the raceme): leaves narrowly linear-oblanceolate, 1–2^{cm} long; the lower tapering into the slender petioles: raceme at length open and long for the plant: sepals purplish-green, linear-oblong, subacute, 4–5^{mm} long: the spatulate-obovate petals nearly twice as long, the upper half of the blade a fine purple, shading into the yellow of the lower half and the claw: silique globose, 4–5^{mm} in diameter; the slender style as long and the ascending or often recurved pedicel usually distinctly longer.

Dr. *J. Lunell*, of Leeds, N. D., an enthusiastic student of the northwest flora, communicated the specimens to me. I have pleasure in naming the species in his honor. He writes: "It grows on high barren hills among rocks. Its petals are broadly purple-tipped, and the base a bright-yellow." Collected at Butte, Benson Co., N. D., June 13, 1905.

Lepidium Zionis, n. sp.—Glabrous perennial, 1–2^{dm} high: stems several from the crown of a rather thick semi-fleshy vertical root, decumbent at base but assurgent-erect, each ~~corymbosely~~ branched at summit: all the leaves erect, quite entire, thick or subcoriaceous, acute or apiculate; radical leaves oblong, 2–3^{cm} long, tapering to a slender petiole as long as the blade; cauline leaves very numerous, almost imbricated, linear-lanceolate, 15–25^{mm} long: racemes short, crowded: sepals elliptic, scarious margined, half as long as the obovate-cuneate white rather conspicuous petals: stamens 2: silique ovate or elliptic, somewhat keeled, glabrous, not emarginate; the style and small stigma one-fourth as long.

This quite unusual species rests upon but one collection at present, *M. E. Jones'* no. 5411, Richfield, Utah, June 13, 1894.

Cardamine incana (Gray), n. n.—*C. cordifolia incana* Gray, Jones in Proc. Cal. Acad. Sci. II. **5**:620. 1895; *C. cardiophylla* Rydb. Bull. Torr. Bot. Club **28**:280. 1901; not *C. cardiophylla* Greene, Man. Bot. 19. 1894.

Euphorbia Aliceae, n. sp.—Perennial from slender horizontal rootstocks, glabrous or slightly puberulent, 10–15^{cm} high: stem branching from the base, the branches spreading-decumbent: leaves narrowly oblanceolate, short-petioled, sharply serrate, opposite, more crowded toward the terminal clustered involucres: involucres nearly sessile, small, turbinate, somewhat fimbriate-margined; the glands about 4, small, short-stipitate, sometimes minutely cornuate or even obscurely appendaged: capsule glabrous: seeds subcubical, with a caruncle, slightly tuberculate, ashy.

Known as yet only from Hartville, Wyoming, no. 549, collected July 15, 1894. Named in honor of Mrs. *Celia Alice Nelson*, whose industry as a collector is responsible for thousands of specimens found in the leading herbaria, although her name has never appeared on a plant label.

Delphinium Cockerelli, n. sp.—Tawny-pubescent on stems and in the inflorescence, densely and viscidly so above; the leaves obscurely pubescent: stems nearly simple or bushy-branched, 6–12^{dm} high: leaves large, often 12–18^{cm} in diameter, the veins strikingly superficial, about 5–cleft or parted into broadly oblong or oblong-cuneate divisions, these merely coarsely toothed or incised above the middle: racemes often several, open, with rather long peduncles and pedicels and few flowers (5–10): flowers bright-purple, large (3–4^{cm} long): sepals oblong-lanceolate, acute, about as long as the thick curved spur: petals small; the upper yellowish-white, concealed within the upper sepal; the lower purple, with suborbicular blade, cleft and sparsely hirsute ciliate.

An unusually handsome species, with somewhat the aspect of *A. subalpinum* (Gray) A. Nels. Bull. Torr. Bot. Club **27**:263. The type was collected by Mrs. *O. St. John*, no. 90, Baldy Mts., Elizabethtown, N. M., Oct., 1898. It was communicated to me by Professor Cockerell, who called my attention to some of its distinguishing characters. *C. F. Baker's* no. 325, near Pagosa Peak, Colo., is also quite typical.

Aconitum lutescens, n. sp.—Root small, fusiform-tuberous: stems slender, simple, erect, only 3–6^{dm} high, glabrous nearly to the inflorescence: leaves 3–5^{cm} broad; the 5 broadly cuneate divisions deeply and incisely toothed above the middle: raceme narrow, long for the plant, rather open; the flowers a pure cream-color, becoming nearly white or pinkish in drying; rachis and pedicels softly hirsute-ciliate with straight viscid hairs standing out at right angles.

This Aconitum with its fine cream-colored flowers may best stand as a species. Collections of it are as follows: *Aven Nelson*, no. 1521 (type), Cummins, Wyo., July 1895; *T. D. A. Cockerell*, no. 87, Beulah, N. M., 1898; *W. S. Cooper*, no. 274, Estes Park, Colo., July 1904.

Anemone zephyra, n. sp.—Green but sparsely long-pilose: stems one or more from the thick erect caudex, 7–15^{cm} high, rather stout: basal leaves petioled, ternate, the broad petiolulate segments in turn deeply incised into linear-oblong lobes; involucral leaves sessile, with linear-oblong lobes: flowers large, 2–3^{cm} broad, lemon-yellow or ochroleucous, usually solitary and rather long-pedunculate, sometimes umbellately 2–4–flowered: achenes large, glabrous, obovate, tapering to a stipe-like base, tipped with the short hooked style.

There seems to be no good reason for continuing the name *A. narcissiflora* for this plant of the central Rocky Mountains. That Arctic species is white-flowered, the flowers very closely umbelled in the involucre, and the leaves are cleft into many more lobes than ours. The proposed species probably includes all the specimens from the Rocky Mountains of the United States distributed as *A. narcissiflora* or *A. albomerus* (ined.).

Anemone stylosa, n. sp.—Low from a thickened simple or branched caudex densely covered with the dead sheathing petioles: basal leaves pale green, glabrous, biternate, segments 3-parted, again incised into linear-lanceolate acute lobes; involucral leaves short-petioled, otherwise quite similar: stems and petioles sparsely long-pilose, the hairs spreading or refracted: sepals oval or oblong, purplish red or greenish red: achenes pubescent, with rather long straight glabrous persistent styles hooked at the tip.

This I take it is the plant referred to *A. tetonensis* in Syn. Fl. N. A. **1**:10. As yet reported only from type locality, Fish Lake, Utah, *M. E. Jones*, nos. 5763 and 5764, Aug. 7, 1894.

Clematis plattensis, n. sp.—Stems clustered on the crown of a thick woody root, 12–18^{cm} high, terminated by the single stout peduncle of nearly equal length in fruit, sparsely short-villous: basal leaves small, scale-like and entire: foliage proper of about 3 pairs of nearly simply pinnate short-petioled leaves; pinnae 7–9, the lowest pair sometimes ternate, all distinctly petiolulate (petiolule 3–10^{mm} long) and long-villous: achenes long-tailed, hairy-plumose: flowers not known, presumably much like those of *C. Douglasii.*

Type from the North Platte Cañon, in eastern Wyoming, *Aven Nelson*, no. 8355, July 2, 1901.

RANUNCULUS JOVIS A. Nels. Bull. Torr. Bot. Club **27**:261. 1900.

This it turns out is *R. digitatus* Hook., an untenable name, as it is antedated by *R. digitatus* Willd. *R. Jovis* will therefore have to stand for Hooker's plant.

Ranunculus platyphyllus (Gray), n. n.—*R. orthorhynchus platyphyllus* Gray, Proc. Am. Acad. **21**:377. 1886; *R. maximus* Greene, Bull. Torr. Bot. Club **14**:118. 1887.

There seems to be no good reason why Dr. Gray's name should have been rejected.

Saxifraga oregonensis (Raf.) n. n.—Diminutive perennials from a slender caudex: stems simple, 3–8^{cm} high, glandular-pubescent: the leaves small, mostly basal, oblong-spatulate, minutely hispid-ciliate: flowers few, in a crowded glomerule at summit: calyx minutely glandular-pubescent, its whole tube adnate to the carpels: petals broadly obovate-cuneate, truncately rounded at summit, twice as long as the calyx lobes, distinctly divergently 3-nerved: the distended subglobose calyx-tube papillose-rugose from the pressure upon it by the numerous brown seeds within.

This is the rare and troublesome little alpine plant of the middle Rocky Mountains which has been referred to *S. adscendens* L., an arctic plant from which it seems to be distinct. The other names which it has also borne are *S. petraea* L. and *S. controversa* Sternb., both of which seem to refer to *S. adscendens* L., and are furthermore both encumbered by synonyms through their application to other very distinct species. Therefore it seems best to take up Rafinesque's name, under Ponista (*P. oregonensis* Raf. Fl. Tellur. **2**:66. 1836), as there can be no doubt as to its application to our plants.

SAXIFRAGA SUBAPETALA **normalis**, n. var.—Very similar to the species, but petals evident, elliptic-spatulate, as long as the calyx-lobes: as in the species the carpels are immersed in a crest-margined disk which persists at the middle of the mature carpels as an undulate ridge.

For the description of the species see Erythea **7**:169. 1899. This has been distributed by various collectors either as *S. integrifolia* or as *S. Sierrae*, from both of which it is quite distinct.

Parthenocissus laciniata (Planch.), n. comb.—*P. quinquefolia laciniata* Planch. in DC. Mon. Phan. **5**:449. 1887; *P. vitacea* (Knerr) A. S. Hitch., Sp. Fl. Man. 26. 1894.

Prunus ignotus, n. sp.—Shrubby or possibly becoming tree-like: branches slender, none of them becoming indurated or thorny: leaves glabrous from the first, simply and sharply serrate: flowers white, appearing with or after the leaves, solitary or 2–3 in a cluster: calyx turbinate; its lobes entire, glabrous within and nearly so without: petals obovate: fruit not known.

It is a little singular that no one has reported this in fruit, but the fine specimens distributed by Prof. *C. S. Crandall*, as *P. pennsylvanica*, from the banks of the Cache la Poudre, near Ft. Collins, Colo., May 1897, cannot well be ignored.

Philadelphus intermedius, n. sp.—A low branching shrub with dark green glabrous aspect: leaves short petiolate or subsessile, broadly oval to ovate, rounded at base and either subacute or obtuse at apex, entire, glabrous or with some scattering ciliate hairs closely ciliate on the margins with short incurved hairs, 15–25^{mm} long: flowers medium size, a 3-flowered cyme from the terminal pair of leaves, a pair of flowers in the next pair of leaves, and sometimes another pair in the axils of the next lower pair of leaves—thus all the flowers except the terminal one are foliose-bracted: calyx glabrous, its lobes finely pubescent within: petals oval, about 12^{mm} long: stamens 30 or more: styles united for two-thirds of their length, the free portion as long as the abruptly enlarged stigmatic portion.

This is most nearly allied to *P. Lewisii* Pursh, from which its smaller size, smaller leaves, smaller flowers, and peculiar stigmas distinguish it. In *P. Lewisii* the styles are united throughout, the stigmatic portion as long as the style proper, the stigmatic line being broad and capping the summit of the stigma and then extending down to the styles in a narrowing line. *P. intermedius* seems to be a connecting species between the desert species of Utah and Colorado and those larger forms of the humid northwest.

Philadelphus nitidus, n. sp.—Slenderly and divaricately branched: leaves rather few, shining and with glaucous hue on both sides, nearly glabrous above, minutely appressed strigose below, mostly narrowly lance-oblong, subacute at both ends, very short petioled, 1–2^{cm} long: flowers generally solitary at the ends of the branchlets: calyx cleft below the middle, hirsute on the outside, soft pubescent on the inside of the lobes: petals elliptic, entire, 8–10^{mm} long, twice as long as the calyx lobes: stamens 30–40: styles distinct down to the ovary: stigmas short, slightly geniculate at junction with filament.

The following collections of this species are at hand: *H. N. Wheeler*, no. 425 (type), Sapinero, Colo., 1898; *C. F. Baker*, no. 266, Black Cañon, Colo., June 27, 1901; *M. E. Jones*, no. 6303, Belknap, Utah, June 28, 1899.

LARAMIE, WYOMING.

BRIEFER ARTICLES

ANTHOCEROS AND ITS NOSTOC COLONIES.

The association of the liverwort Anthoceros with the blue-green alga, Nostoc, has long been known and has been studied with considerable care. The significance and value of this association have been speculated upon; but, as far as I know, no experiments on the subject have been reported. The anatomical relations of the two associates have been studied and described, but I do not know that cultures of Anthoceros from the spore on sterilized soil have been attempted. I shall here describe both the culture of Anthoceros, and, at the risk of some repetition of facts already recorded by others, the anatomical relations of the Nostoc to the surrounding tissue.

Anthoceros fusiformis Aust., and *A. Pearsoni* M. A. Howe fruit here abundantly in May. Their spores can then be collected almost or quite unmixed and free from the spores of other small plants, and may be kept air-dry for months. The dry season ordinarily lasts from mid-May to October, and during this time usually no rain falls. The spores germinate out of doors soon after the first abundant rain has thoroughy moistened the soil to a depth of several inches. The natural "resting-period" for the spores is, therefore, four or five months long, but the spores retain their vitality much longer. They may also be made to germinate in much shorter time. The "resting-period" seems to be, therefore, a matter of natural conditions rather than of transmitted habit.

The soil on which I grew plants from the spore was brought into the laboratory from the bank on which these plants, along with other small archegoniates, grow abundantly during each rainy season. After thorough air-drying, the soil was freed from pebbles, pulverized in a mortar, and put to a depth of a centimeter or slightly more in crystallizing dishes of thin white glass. These dishes were about 8^{cm} in diameter, 3.5^{cm} in depth, and were covered by the lids or bottoms of Petri dishes. These covers do not fit tightly; at the same time that they exclude dust and maintain the moisture of the air, they permit fair ventilation. The soil was invariably moistened from the beginning with boiled distilled water, for I wished to avoid any accumulations of salts in these undrained cultures from using our hard tap-water. These covered dishes were now divided into two lots of equal number, one lot being put aside in the dark for a few days and the other steam-sterilized for two or three hours on three successive days. This sterilization proved thorough so far as blue-green algae are concerned, since none developed in the dishes. A certain amount of infection is unavoidable, and a few cultures in each lot had to be thrown away because of the development of some "damping-off" fungus. But on the whole the plants in my cultures have done quite as well as those out of doors. During the growing season now ending they did better than those out of doors, because November and December were cold and dry.

Eleven or twelve weeks after sowing, the small plants already bear archegonia and antheridia when the cultures are kept under suitable conditions of illumination. Cultures kept too dark will contain few if any fruiting plants, though the plants may be normally large. From this fact, though I have not attempted to support this view by further investigation, one may infer that light acts as a stimulus to the development of the reproductive organs as VÖCHTING[1] and KLEBS[2] have shown to be the case in certain flowering plants and fresh-water algae.

On comparing the young plants on sterilized and on unsterilized soil the greater size and more robust appearance of the plants on sterilized soil is evident. The plants on sterilized soil contained no Nostoc colonies. The plants on unsterilized soil contained Nostoc colonies, few of them bore reproductive organs, and they appeared less thrifty. But the young Anthoceros plants on unsterilized soil were obliged to compete not only with each other but with several other sorts also. Without attempting an exhaustive list of these other plants I may record the presence, in the cultures, of prothalli of *Gymnogramme triangularis*, fronds of *Fimbriaria Californica*, two or three small mosses, both protonemal and adult, some green algae (especially a small Vaucheria), some blue-green algae (Nostoc, Oscillatoria, Anabaena), chickweed, and grass. Besides these, which started from spores, seeds, or other resting stages, there were small plants which had held over the dry season as CAMPBELL[3] has described, fern prothalli and plants of Fimbriaria and Anthoceros.

Where young plants of Anthoceros have to compete in small cultures with such a number of individuals and of kinds of already fairly established plants, it is natural to assume that this amount of competition may

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[1] VÖCHTING, H., Ueber den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüthen. Jahrb. Wiss. Bot. **25**: 149. 1893.

[2] KLEBS, G., Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen. Jena, 1896.

[3] CAMPBELL, D. H., Resistance of drought by liverworts. Torreya **4**: 81. 1904.

have much to do with their less thrifty appearance. However, the presence of Nostoc colonies on the soil does not necessarily imply the infection of all Anthoceros plants near them. As a matter of fact, a good many Anthoceros plants free from Nostoc can be found on unsterilized soil. These look better than those beside them containing Nostoc colonies, and as well as those in the dishes of sterilized soil.

Where cultures receive light mainly from the side, as is generally the case in a laboratory, Anthoceros plants, like fern-prothalli and the thalli of Fimbriaria, turn up from the surface of the soil, presenting their normally upper surface toward the window and bearing rhizoids on the shaded side. These plants necessarily contain fewer Nostoc colonies than those remaining flat on the soil, for the younger and elevated parts are less accessible to Nostoc filaments. Comparisons of older cultures than those just described shows that Anthoceros plants containing only one or two algal colonies are nearly or quite as thrifty as those with none, and are decidedly more vigorous than those with many.

Prantl[4] attributed an advantage to Anthoceros from its association with Nostoc, on the ground that Nostoc might fix the free nitrogen of the air and contribute its products to the liverwort, but the weight of evidence seems now to be against the assumption that blue-green algae by and of themselves add at all to the combined nitrogen in the soil,[5] whatever the results of their association with N-fixing soil bacteria may be. The fact that, in my cultures at least, Anthoceros does better when free from Nostoc, removes all ground for Prantl's claimed advantage from the association so common in nature.

On the other hand Janczewski's designation of the Nostoc colonies as parasitic[6] is not logically justified by my cultures or by the luxuriance in growth and by the fertility of these two species of Anthoceros in this region in ordinarily good seasons. Last year they throve as I never saw them before. This season has been by no means so favorable, dry weather having come long before the plants, held back by the cold and dryness of November and December, could ripen their spores in large numbers. All I feel inclined to say is that Nostoc certainly does not benefit Anthoceros, which in fact does better without it.

It is a matter of common observation that many blue-green algae

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[4] Prantl, K., Die Assimilation freien Stickstoffs und der Parasitismus von Nostoc. Hedwigia **28**:135. 1889.

[5] Pfeffer, W., Pflanzenphysiologie, 2te Auflage, **1**:386–7, 393. 1897.

[6] Janczewski, A. de, Vergleichende Untersuchungen über die Entwickelungsgeschichte des Archegoniums. Bot. Zeit. 377 ff. 1872.

thrive best where there are considerable quantities of organic matter.[7] It is conceivable that Nostoc profits from intimate association with green plants, but to prove the parasitic nature of such association is very difficult. I could not detect that the Nostoc cells, filaments, and colonies within the thallus of Anthoceros appear healthier, or larger, or grow more rapidly, than those on the moist earth near by. The cells of this and many other blue-green algae are so small and the organs of the cell so slightly differentiated that differences between cells are by no means noticeable. From the evidence at hand it is equally unsafe to say that Nostoc is or is not parasitic in Anthoceros.

Passing now to anatomical considerations, PRANTL[8] asserts that the characteristic development of the thallus cavities and the formation of internal hairs follows the entrance of Nostoc filaments only, not of any other small plants. The manner of infection I will not go into, for it has been repeatedly described.[9] The invading filament, if it survives, gives rise to a colony, spheroidal in form and enclosed in gelatinous matter which increases with the growth of the colony. Mechanical pressure, increasing with the growth of the colony and with the amount of water absorbed, is brought to bear against the surrounding cells of the thallus, enlarging the cavity which the Nostoc filament entered through one of the slime-slits on the surface. Another effect of the increasing pressure is the compacting of the immediately surrounding tissue. But because the Nostoc colony is not homogeneous, being in part cells and in part the gelatinous product of these cells, the pressure is not equal over all parts of the surface. The gelatinous matter between the filaments is softer and more readily penetrated or displaced than the filaments themselves. If small thallus cells lie opposite to and in contact with these gelatinous parts of a colony, they will necessarily be pushed forward by their neighbors. As has long been known, chains of cells, constituting the internal hairs above mentioned, do grow into the colonies and among the filaments of Nostoc. Other organisms, though they may enter the body of the liverwort, either do not exert any pressure at all, being smaller than the cavities they occupy, or form such compact masses that there is no chance for the surrounding cells to grow out as chains.

From this consideration of the structure and mechanics of the Nostoc colony, we are led to see the fallacy of PRANTL's argument that, because

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[7] See for example KIRCHNER, O., Schizophyceae in Engler & Prantl's Natürliche Pflanzenfamilien. I. 1^a:48. 1898.

[8] PRANTL, K., *loc. cit.*

[9] CAMPBELL, D. H., Mosses and Ferns, Ed. 2, 128. New York, 1905.

cavities and hairs do not develop in the familiar way except where Nostoc colonies are, the liverwort must profit by such associates. It is simply a matter of mechanics. Where the resistance is less than growth can overcome (and this is the case between the Nostoc filaments in the gelatinous mass), the liverwort cells will grow out, forming short hairs. The growing and swelling colony as a whole will enlarge the cavity in which it lies. There are other intercellular spaces throughout the thallus, but these are not enlarged because not occupied. There is no conceivable advantage in their enlargement.—GEORGE J. PEIRCE, *Stanford University, California.*

DISTRIBUTION AND HABITS OF SOME COMMON OAKS.

SINCE writing the paper under this title, which appeared in the June number of this journal, I have been in Milwaukee and had the opportunity of examining the oaks in two herbaria, probably representative of any that may be found there. In the Public Museum were two specimens labeled *Quercus palustris* Du Roi. One had an acorn, and as far as determinable by this and the leaf-characters, was *Q. ellipsoidalis;* it is certainly *not* what it is labeled. The other was without fruit, and was doubtless the same species. In the herbarium of Dr. LEWIS SHERMAN, one of the older residents of Milwaukee and an acquaintance of Dr. LAPHAM, was a specimen labeled as above. It had an acorn cup but no nuts. This showed at least that it was *not Q. palustris.* All the evidence tends to the conclusion that the real pin oak does not occur in the region from which these specimens were taken.—E. J. HILL, *Chicago.*

CURRENT LITERATURE.

BOOK REVIEWS.

Evolution.

A comprehensive account of the subject of evolution is at present a matter of considerable importance, but at the same time must be one of unusual difficulty because of the great activity incited by the work of de Vries and others who have within the last few years undertaken the study of variation, adaptation, and heredity by experimental methods. Dr. J. P. Lotsy[1] has undertaken this most difficult task by the publication of a volume of lectures upon theories of descent with special reference to the botanical side of the question. He follows the method not infrequent among older writers but rare among writers of recent scientific works, of beginning at the beginning. He first considers the nature of knowledge, and the supposed conflict between science and religion, pointing out that evolution will not explain everything, and that there is no conflict between religion and science except as either or both attempt to explain dogmatically the unexplainable. Both science and religion come to the same conclusion when traced to their limit, namely, that there is a fundamental mystery incapable of investigation because none of the possible alternatives is even conceivable to the human mind.

After these two introductory lectures, one lecture is devoted to evolution in general, beginning with the origin of the earth, the evolution of minerals, the origin of life, and the relation of form to environment. Two lectures deal with the morphogenic stimuli and the various theories of direct response and adaptation. The views of Reinke and Klebs are contrasted, and those of Lamarck, Spencer, Nägeli, and Warming are compared. Here the author gives a well-deserved appreciation of the work of Lamarck, though he is not himself in any proper sense a Lamarckian. The subject of heredity is considered in six lectures, dealing first with the older theories of Spencer, Darwin, Nägeli, and Weismann, which were of a purely hypothetical nature, and then taking up the development of our knowledge of chromosomes as the bearers of heredity. One whole lecture is devoted to Mendel and his laws, two to variation curves and Galton's laws of inheritance, and one to numerous subsidiary questions, such as dominance and blending, atavism, kryptomery, pleiotypy, half races, etc., and one to the inheritance of acquired characters.

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[1] Lotsy, J. P., Vorlesungen über Descendenztheorien mit besonderer Berücksichtigung der botanischen Seite der Frage, gehalten an der Reichsuniversität zu Leiden. Erster Teil. 8vo. pp. xii+384. *pls. 2. figs. 124.* Jena: Gustav Fischer. 1906. *M* 8; geb. *M* 9.

Discontinuous variation and mutation are treated in three lectures, and the six remaining lectures trace the history of the evolution idea from ARISTOTLE to DARWIN, the last lecture being devoted to the life of the latter.

A treatise on contemporaneous science is fraught with the same difficulties as attend the writing of contemporaneous history. A just estimate of the importance of the latest developments in either case only becomes possible in the light of subsequent development, and consequently a book of this kind might be expected to have a very evanescent value. LOTSY has avoided very much of this by taking a judicial attitude and treating his subject historically. He has depended to a very large extent upon quotations from the various scientists whose views or results he has presented, and this gives the reader something of the unpleasant sensation always given by a so-called "digest;" but his choice of quotations is good and his own language is simple and direct, and therefore easily followed.

A second volume is promised, in which is to be indicated the work still to be done, and this will be awaited with much interest, for it will be here that we may hope to gain more of the personality of the author. The present volume is exceptionally impersonal, and both gains and loses by this fact. If the second volume takes on the strength and virility of personal enthusiasm which incites to investigation, the lack of such qualities in this first volume may not be looked upon as a disadvantage. But even if it should indicate in the same dispassionate manner that characterizes this book, the problems awaiting solution, he will deserve the gratitude of every biologist. While this book can not be said to *fill* the need that called it forth, it is gratifying that the first attempt at filling it is so excellent. As the first comprehensive work dealing with the more recent phases of evolutionary study it should at once gain a deservedly large circulation.—GEORGE H. SHULL.

Chemistry of plants.

THE second volume of CZAPEK'S *Biochemie der Pflanzen* is a huge one,[2] and deepens the impression made by the first volume of the immense labor which such a compilation represents, and the equally immense service which the author has rendered to science in its preparation. For knowledge of the chemistry of plants has lagged far behind that of animals, which, under the stimulus of human relations through medicine, has been under constant investigation by many students.

This volume is devoted to (1) the proteids and their metabolism in various plants (bacteria and fungi, mosses, algae, seeds, buds, leaves, roots, pollen grains) including the formation, absorption, and regeneration of proteids by various parts and under various conditions; (2) the nitrogenous end products of metabolism, including purin bases, glucosides yielding HCN, and alkaloids;

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[2] CZAPEK, F., Biochemie der Pflanzen. Zweiter Band. 8vo. pp. xii+1027. Jena: Gustav Fischer. 1905. *M* 25.

(3) respiration and its products; (4) coloring matters other than chlorophyll and its associates; (5) mineral constituents; and (6) substances produced by stimulation. At the close is an appendix of 21 pages with many supplementary notes and corrections, bringing the data down to June 1905. A complete index renders available the rich store of information summarized in the text, and gives thus a clue to the literature of any substance or the chemistry of any group of plants.

The work is rather more than its title indicates, since it is pervaded by a strong physiological flavor. The chapter on respiration, indeed, is almost as much physiological as chemical, though it deals chiefly with the quantitative relations of the oxygen fixed and the various end-products of "oxidation."

With this work as a convenient register of the work heretofore done in plant chemistry, the progress of knowledge in this field ought to be much accelerated. Even though no such chemical work is in progress, every botanical laboratory, whether in experiment station or college, and every chemical laboratory, in connection with its courses or work in organic chemistry, needs this book for reference; while for public libraries it is as indispensable as an encyclopedia.—C. R. B.

MINOR NOTICES.

Mosses.—The third part of GROUT'S *Mosses with hand-lens and microscope* contains the families Encalyptaceae, Orthotrichaceae, Funariaceae, Bryaceae, Leskeaceae, and some of their smaller allies.[3] The Orthotrichaceae and Bryaceae are particularly difficult groups, and the admirably reproduced illustrations from the *Bryologia Europaea* and SULLIVANT'S *Icones* (with an occasional original figure) will be most helpful to amateurs who cannot own these costly works. The keys are clear and concise. The text might easily be improved by being made more formal, with the chatty matters reduced to notes in smaller type under the appropriate headings. But the clientèle to whom the work is addressed will not quarrel with this—until they become increasingly expert and seek data for which the space might have been used but is not. Then it will be time for them to lay aside these useful crutches and take up the technical works. It is a marvel that the author can furnish such numerous and good illustrations and well-printed letter-press at the price.—C. R. B.

Sylloge Fungorum.—Volume XVIII, Part VII of the Supplement of that monumental work of taxonomic mycology, Saccardo's *Sylloge Fungorum*, has recently been issued (January 30, 1906). This volume contains additions bringing as nearly up to date as possible the compilation of descriptions of the Discomycetae, Myxomycetae, Myxobacteriaceae, and Deuteromycetae. The last group, which constitutes the *Fungi Imperfecti* of the older volumes, occupies fully

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[3] GROUT, A. J., Mosses with hand-lens and microscope, a non-technical handbook of the more common mosses of the northeastern United States. Part III. Imp. 8vo. pp. 167–246. *pls. 36–55. figs. 79–133.* Brooklyn, N. Y. The Author, 360 Lenox Road. 1906. $1.25.

two-thirds of the present volume. The work concludes with the usual "repertorium," index of species, and a complete index of genera in all volumes. The generic index is printed on differently colored paper. Some suggestions regarding the diagnosis and nomenclature of species printed in the first pages of the volume aim to bring about some uniformity in the publication of species. As these rules have been published in several journals,[4] it is unnecessary to repeat them here.—H. HASSELBRING.

A book for young gardeners.—A booklet prepared by H. D. HEMENWAY,[5] the director of the School of Horticulture at Hartford, Conn., will prove helpful to those interested in home and school gardens. Aside from simple discussion of the objects and benefits of tillage, the preparation of the soil, and planting the garden, the booklet furnishes abundant and detailed directions for testing and saving the seeds of the more common flowers and vegetables, for the planting of trees, the making of hot-beds, the making of window gardens, and for the culture of strawberries and other fruits. The directions are clear and give with sufficient detail the points most useful to the beginner.—H. HASSELBRING.

Das Pflanzenreich.—Part 25 of this work has just appeared[6] and contains a presentation of the Juncaceae by the late Dr. FR. BUCHENAU. The usual full discussion of the various structures of the family and its geographical distribution is followed by a synopsis of the 8 genera, among which the species are distributed as follows: Distichia (3), Patosia (1), Oxychloe (2), Marsippospermum (3), Rostkovia (1), Prionium (1), Luzula (61, of which 2 are new), Juncus (209, of which 5 are new). The whole presentation is remarkably full in details of forms and in illustrations, and is of particular interest to American botanists.—J. M. C.

Index Filicum.—The ninth fascicle of CHRISTENSEN's work has appeared,[7] carrying the references from *Polypodium Beddomei* to *Polystichum aculeatum*. The great genus Polypodium fills the whole fascicle excepting the last page.—J. M. C.

NOTES FOR STUDENTS.

Plant diseases.—CLINTON,[8] in his report as Botanist of the Connecticut Experiment Station for 1905, presents interesting notes and illustrations of several fungous diseases of plants in that state, followed by a more detailed

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[4] In the United States, in Jour. Mycol. **10**:109. 1904.

[5] HEMENWAY, H. D., Hints and helps for young gardeners, a treatise designed for those young in experience as well as youthful gardeners. 8vo. paper. pp. 59. illustrated. Hartford, Conn.: The Author. 1906. 35 cents.

[6] ENGLER, A., Das Pflanzenreich. Heft 25, Juncaceae by FR. BUCHENAU. 8vo. pp. 284. *figs. 121 (777)*. Leipzig: Wilhelm Englemann. 1906. *M* 14.20.

[7] CHRISTENSEN, C., Index Filicum, etc. Fasc. 9. Copenhagen: H. Hagerups Boghandel. 1906. 3*s*. 6*d*.

[8] CLINTON, G. P., Report of the Botanist. Rept. Conn. Exp. Stat. **1905**: 263–330. *pls. 13–25. figs. 8–9.* 1906.

account of the downy mildew of the lima bean, due to *Phytophthora phaseoli*, and of the downy mildew or blight of the Irish potato, due to *Phytophthora infestans*. The two latter diseases are fully described and illustrated, and citations of the literature of each disease are given.

Whetzel[9] gives an illustrated account of the following bean diseases found in New York state: anthracnose, due to *Colletotrichum lindemuthianum*; blight, due to *Bacterium phaseoli;* and rust, due to *Uromyces appendiculatus*. Methods of treatment are also given in each disease.

Sheldon[10] has just published the results of his study of the ripe rot or mummy disease of guavas. This disease is similar in many respects to the ripe rot or bitter rot of apples. It is produced by *Glomerella psidii* (G. Del.) Sheldon. He found the ascigerous stage and worked out the life history of the fungus in considerable detail.

Norton[11] has published a brief summary of the present knowledge of the diseases of the Irish potato in Maryland together with methods of treatment of these diseases.

Stevens[12] in his report as Biologist of the Experiment Station of North Carolina gives the results of his experiments in soil treatment for the prevention of the Granville tobacco wilt. He concludes that the greatest hope of overcoming this serious trouble lies in the breeding and selecting of resistant strains of tobacco, and he is now engaged in this line of work.

Smith[13] presents preliminary observations regarding three serious diseases of tomatoes in California. The first is the damping off of the young seedlings. It is suggested that to check the spread of this trouble the plants and soil be sprayed with weak Bordeaux mixture followed with a sprinkling of sulfur. Soil sterilization by means of live steam would no doubt control it in cases where the application of this remedy is possible. The second disease mentioned is the summer blight, due to a species of Fusarium which attacks the plant in much the same manner as does the fusarium stage of Neocosmospora which causes the wilt of cotton, etc. The third disease mentioned is the winter blight, due to the potato-blight fungus, *Phytophthora infestans*. It occurs only after heavy fogs, dews, or rains, and hence in California attacks only the winter crop. Spraying with Bordeaux mixture is recommended to be applied just after the rains or dews.

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[9] Whetzel, H. H., Some diseases of beans. Bull. N. Y. Cornell Exp. Stat. 239:195–214. *figs. 100–114.* 1906.

[10] Sheldon, J. L., The ripe rot, or mummy disease of guavas. Bull. W. Va. Exp. Stat. 104:299–315. *pls. 1–4. fig. 1.* 1906.

[11] Norton, J. B. S., Irish potato diseases. Bull. Md. Exp. Stat. 108:63–72. *figs. 1–4.* 1906.

[12] Stevens, F. L., Report of the Biologist. Rept. N. Car. Exp. Stat. **1904**: pp. 10. 1905.

[13] Smith, R. E., Tomato diseases in California. Bull. Calif. Exp. Stat. 175: 1–16. *figs. 1–8.* 1906.

Reed[14] has described three fungous diseases of the cultivated ginseng. These diseases are not due to the same fungi reported by Van Hook[15] as causing ginseng diseases in New York. The first of these is a stem anthracnose due to *Vermicularia dematium.* The second is a leaf anthracnose due to *Pestalozzia funeria.* These two diseases he finds may be controlled by spraying with the usual Bordeaux mixture. The third disease described is a wilt due to *Neocosmospora vasinfecta nivea.* This same variety causes a wilt disease of the watermelon, while the species itself causes a wilt disease of cotton and the cowpea. Reed finds that the wilt never occurs except in association with or following an attack of the stem anthracnose. In other words, the wilt fungus seems to be able to gain entrance to the ginseng plant through the lesions on the stem due to this other stem disease. It is also possible that the wilt fungus enters the plant at the scar left where the stem of the preceding year fell off. It should be recalled in this connection that the cotton and cowpea wilt-fungus enters the host through the roots largely after injury by the nematode worm.—E. Mead Wilcox.

Sorauer[16] describes a peculiar disease of *Cereus nycticalis* Lk. which results from proliferation of cells of the inner layers of the cortex. This produces on the stems slightly elevated hygrophanous areas which increase in size until they occupy a large part of the stem and extend to the wood. These turn brown and then black and finally collapse, leaving depressed wounds in the stem. On account of the position of the proliferating cells Sorauer designates these growths as "internal intumescences." The diseased regions are almost free from starch, but they are rich in glucose, which the writer regards as the cause of the unusual growth. This condition is brought about by high temperature and excessive moisture. When these factors were changed no "intumescences" were formed. —H. Hasselbring.

The maturation mitoses.—A critical review of the entire subject of the maturation mitoses in both plants and animals has been prepared by Grégoire.[17] Part I, dealing with stages from the metaphase of the first mitosis in the mother-cell up to the telophase of the second division, contains 155 pages and 147 text figures, of which 35 pages and 35 figures relate to sporogenesis in plants, 90 pages and 112 figures to spermatogenesis and oogenesis in animals, and the remaining 30 pages to a comparative study. The space given to animal mitoses increases the value of the work to botanists, who are already more or less familiar with the botanical literature. At the close of the botanical section the conclusion

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[14] Reed, H. S., Three fungous diseases of the cultivated ginseng. Bull. Mo. Exp. Stat. 69:41–66. *figs. 1–9.* 1905.

[15] Van Hook, J. M., Diseases of ginseng. Bull. N. Y. Cornell Exp. Stat. 219: 163–186. *figs. 18–42.* 1904.

[16] Sorauer, P., Zeitr. Pflanzenkrankheiten **16**:5–10. *pl. 2.* 1906.

[17] Grégoire, Victor, Les resultats acquirés sur les cinèses de maturation dans les deux règnes. Premier mémoire. Revue critique de la littérature. La Cellule **22**:221–376. *figs. 147.* 1905.

is reached that the definitive chromosomes of the first mitosis constitute two branches which are variously placed with relation to each other. These two branches are the daughter chromosomes of the first mitosis. During the metaphase or anaphase these daughter chromosomes split longitudinally. In the telophase no complete spirem is formed nor do the nuclei reach the resting condition, but the chromosomes preserve their individuality so that the longitudinal portions which appeared in the anaphase of the first mitosis become the daughter chromosomes of the second mitosis. Consequently, the second mitosis cannot be a reduction division. Whether a reduction takes place at the first mitosis will be discussed in the second memoir. In the general résumé the conclusion is reached that in both plants and animals the definitive chromosomes of the first mitosis, at the equatorial plate stage, are composed of two continuous branches. There are two categories of theories as to the significance of the second mitosis, the one holding it as an equation division and the other as a reduction division.

In regard to the two constituent branches of the chromosomes of the first mitosis, there are two possibilities: if they are longitudinal pieces of a segment of a primary chromosome, the heterotypic division is an equation division; if, on the other hand, each of the two branches is a complete somatic chromosome, there is a true reduction in the WEISMAN sense. The important question is, How are the chromosomes of the first mitosis formed? This will be the subject of the second memoir.

The work will be welcomed by cytologists, for the subject matter is well arranged and conflicting theories are impartially discussed. While the title indicates only a critical review of the literature, the work is something more, because so much botanical investigation has been done in the writer's own laboratory, and because even the zoological section has not been written entirely from the literature, but from the writer's own preparations and numerous preparations loaned by prominent investigators of animal cytology.—CHARLES J. CHAMBERLAIN.

Nova in hybrids.—As has been already noted[18] in these pages, TSCHERMAK found a large number of instances in which *nova* appeared in hybrid beans and peas, in very definite ratios which were readily related to the ordinary Mendelian ratio. These *nova* were explained by him as characters latent in one of the parental strains, but rendered patent by the energizing effect of the cross-fertilization. CORRENS has adopted[19] for similar *nova* in Mirabilis the hypothesis of CUENOT, which makes such new characters the result of the combined action of two or more pairs of units, the positive member of some or all but one of these pairs of units being invisible because of the absence of the other member of the combination. For example, an albino mouse bred with a brown mouse may produce black offspring, because the albino contains a unit which

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[18] See BOT. GAZETTE **39**:302. Apr. 1905.

[19] See BOT. GAZETTE **40**:234. Sept. 1905.

has the power of changing the gray pigment to black, but this pigment-changing unit will remain invisible so long as the albino is bred only with other albinos.

Under this conception the *novum* is a compound character formed by the combination of equivalent units, instead of a hitherto inactive character rendered active by the stimulating effect of a foreign plasma. TSCHERMAK[20] now assents to the explanation of CUENOT and CORRENS as valid in certain cases, but still maintains that the *nova* of his *Pisum arvense* × *sativum* crosses and others cannot be so explained, because he found no cases in which the offspring were not *all* cryptomeric. TSCHERMAK'S reference to the fact that the *nova* are frequently of atavistic nature, as lending support to GALTON'S "law of natural inheritance," will scarcely be approved, since the explanation of CUENOT and CORRENS would bring these into agreement with typical Mendelian hybrids.

BATESON[21] has likewise adopted the explanation of CUENOT and CORRENS in the interpretation of *nova* in sweet peas and stocks which had been presented[22] in the Second Report to the Evolution Committee, as wholly out of harmony with Mendelian inheritance. These now constitute exceptionally good examples of characters which can only become manifest when two or more units act together. The statement is made that most of the five gametically distinct types which should appear among the white sweet peas and white stocks of these crosses have been recognized, thus answering satisfactorily, in respect to these two species, TSCHERMAK'S contention that the extracted whites were still cryptomeric.

The same explanation is clearly valid for the case reported by CASTLE[23] in which a white guinea-pig crossed with red gave rise to some black offspring, while the "extracted" whites from this cross, when crossed with red, produced no black young.—GEORGE H. SHULL.

Welwitschia.—The full paper on *Welwitschia mirabilis* by PEARSON has now appeared,[24] the abstract of last November having been noted in this journal.[25] The region of this strange plant is so difficult of access that Professor PEARSON is to be commended for the unusual efforts he has put forth to secure material. As it happened, the war in Africa has seriously interfered with his work, so that he was able to secure material of only one day's collecting, but he hopes that when the country becomes more settled he will be able to fill in the gaps.

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[20] TSCHERMAK, E., Die Mendelsche Lehre und die Galtonsche Theorie vom Ahnenerbe. Arch. f. Rass. u. Gesells. Biol. **2**:663–672. 1905.

[21] BATESON, W., SAUNDERS, E. R., and PUNNETT, R. C., Further experiments on inheritance in sweet peas and stocks: Preliminary account. Proc. Roy. Soc. London B. **77**:236–238. 1905.

[22] See BOT. GAZETTE **40**:313–314. 1905.

[23] See BOT. GAZETTE **40**: 385. 1905.

[24] PEARSON, H. H. W., Some observations on *Welwitschia mirabilis* Hooker. Phil. Trans. Roy. Soc. London B. **198**:265–304. *pls. 18–22.* 1906.

[25] BOT. GAZETTE **41**:226. 1906.

The plant is of such unusual interest that his results deserve rather full statement.

The maximum age attained by individual plants is probably much greater than a century; and plants growing in contact readily form natural grafts, into the composition of which several individuals may enter. Pollination is effected, partly, at least, by insects. The development of the spores and of the embryo proceed with remarkable rapidity for a gymnosperm. Microsporogenesis resembles that described for Ephedra and Gnetum; and at dehiscence three nuclei are found in the pollen grain, one of which, probably prothallial, disappears before shedding. The single megaspore mother cell forms the usual linear tetrad, the innermost spore functioning. In the germination of the megaspore there is abundant free nuclear division, and a strong growth of the sac towards the micropyle and into the chalazal region. The formation of cell walls occurs throughout the embryo sac, the cells thus formed often being multinucleate. Each peripheral cell towards the micropyle, containing two to five nuclei, produces a tubular outgrowth which penetrates the nucellar cap like a pollen tube. As this tube advances the nuclei pass into it, and the distance traversed before pollination occurs is considerable. These free nuclei are sexual, and hence the condition is that of Gnetum. These tube-forming cells have been taken for archegonium initials, but it is evident that the tube is only an extension of the prothallium containing free sexual nuclei; and hence PEARSON rightly calls it the "prothallial tube." This is a most satisfactory disposition of a troublesome structure; and we find that in the act of fertilization Welwitschia is even more specialized than is Gnetum.

It is to be regretted that the first stages of embryo-formation were not shown by the material, for the current statements in reference to it are as obscure and meaningless as have been those in reference to the so-called "archegonium initials."—J. M. C.

Mendelism in agriculture.—No other single scientific proposition has elicited so much interest from agriculturists and breeders as MENDEL's laws of inheritance, and the number of more or less satisfactory popular presentations has become large. Several of these have already been noted. TSCHERMAK[26] adds another in a lecture before the German Agricultural Society, in which particular attention is given to the results in the breeding of cereals. Besides the general explanation of Mendelism, he gives tables showing what characters of the several cereals have been found dominant and what recessive. These tables include sixteen pairs of characters in wheat, five in rye, thirteen in barley, and three in oats. A short section is devoted to the technic of crossing, and another to the importance of establishing stations and properly equipping them for carrying on such investigations.

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[26] TSCHERMAK, E., Die Kreuzung im Dienste der Pflanzenzüchtung. Jahrb. Deutsche Landw. Gesells. **20**:325–338. 1905.

HALSTED[27] has also issued a bulletin which gives a good general discussion of Mendelism as exemplified by cooperative experiments in the breeding of corn. In 1904 "Black Mexican" sweet corn was crossed with nearly a full list of the commercial varieties of sweet corn, and the hybrid ears thus obtained were sent to a number of volunteer observers in different parts of the state, who returned samples and notes which are incorporated into this bulletin. The presentation is simple and easily understood, but several unfortunate typographical errors are likely to prove confusing, as when on p. 15 in the table showing what may be expected in the second generation of a cross between large grained flint black, and small grained sweet white, the fourth category (large sweet white) is weighted with the value 9 instead of 3; and again, when on p. 21, line 7, "white" is used for "dark."

An improper emphasis is laid upon the difficulty of freeing the dominant form from traces of the recessive. Thus, he says that after nineteen generations of selection there will still be one recessive grain in each four hundred, adding that "this underlying rule," which appears to hold more or less closely, helps to indicate how difficult it is to eradicate entirely any characteristic that has been introduced in breeding." He seems to have overlooked the importance of VILMORIN's principle of isolation, by which it requires only one more generation to obtain pure extracted dominants than extracted recessives, so that after the *third* generation he need never have another recessive grain appear.—GEORGE H. SHULL.

Inheritance in Shirley poppies.—PEARSON and his associates, with the aid of a number of volunteer observers, have presented a second paper[28] on inheritance in the Shirley poppy. Some of the questions that were left open in the earlier report[29] have been settled. Thus, it was assumed that Shirley poppies both self- and cross-fertilize, and the discussions were based upon that assumption. It is now found that when flowers are enclosed in bags of bolting-cloth or oiled paper, almost no fertilization takes place. Fifty bagged flowers produced seeds in only four, and these gave rise to nine plants. The conclusion is reached, therefore, that seeds taken from unprotected capsules are essentially the result of cross-fertilization; and the correlation of offspring with each other and with their antecedents should be the same as in other populations in which self-fertilization does not occur, as in animals and man. Although the correlation found is somewhat lower than the average for animals, a number of modifying factors are pointed out which would tend to lessen the correla-

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[27] HALSTED, B. D., Breeding sweet corn—cooperative tests. N. J. Agr. Exp. Sta. Bull. 192. pp. 30. *pls. 4, figs. 8.* March 1906.

[28] PEARSON, K., et al., Cooperative investigations in plants. III. On inheritance n the Shirley poppy. Second Memoir. Biometrika **4**:394–426. 1 *pl.* (colored). 1906.

[29] PEARSON, K., et al., Cooperative investigation in plants. I. On inheritance n the Shirley poppy. Biometrika **2**:56–100. 1902.

tion, and the opinion is expressed that there is no reason to believe that the strength of inheritance is any different in Shirley poppies from that in animals.

Another gain is seen in the recognition of the entire plant as the hereditary unit, instead of the separate flowers, the latter view having been maintained in the earlier paper.

The characters used were the number of stigmatic bands, number of petals and petaloid stamens, color of petals, presence of a margin, presence of a basal spot and its color, and wrinkling of the petals. Each of these characters was divided into a number of categories designated in a manner that makes the personal equation a very large factor, *e. g.* with reference to the presence of a basal spot, the classes are "none, none to slight, slight, slight to well-defined, well-defined, well-defined to large, large." The observers found these categories very difficult to separate, and think there is no evidence of allelomorphic characters. They believe that the same is true in many studies made by those who accept MENDEL'S laws of inheritance. It need scarcely be pointed out that seeds secured from unguarded flowers from a field as heterogeneous as one of Shirley poppies could hardly be expected to show evidences of allelomorphic characters.—GEORGE H. SHULL.

Drying of seedlings and sporelings.—RABE finds that germinated seeds and spores resist drying more or less well.[30] With advancing germinative stages and exhaustion of reserve food the resistance to drying diminishes. Seedlings will withstand much longer drying in the air than in a sulfuric acid desiccator. The separated hypocotyl of a seedling always dies upon being fully dried out. The cotyledons are more resistant than the plumule, and of the latter the growing point and the axillary buds are more resistant than the leaves. The separated and dried portions of the seedling, if they are yet alive, are as vigorous in reproducing as the separated portions of the fresh seedling. In spite of the defective storage and marked shrinkage, the seedling of the unripe seed will withstand drying nearly as well as the seedling of the ripe seed. Seedlings of xerophytes are more resistant to drying than those of hydrophytes. The presence of the seed coat is a disadvantage to the dried seedling. Rapid admission of water is more advantageous to the dried seedling than slow admission. Seedlings of related species show no relation in their power to withstand drying. Water-free chemical reagents, as alcohol and benzene, act more harmfully on germinated dried seedlings than on ungerminated dried seeds. The germinated dried as well as the ungerminated soaked seeds are more injured by diluted than by concentrated glycerin. The longer the glycerin acts the greater the injury. The germinated spores of mosses are extremely resistant to drying whether in the air or in a sulfuric acid desiccator. Germinated spores of ferns and liverworts withstand but little drying. The power of plants to withstand drying depends mainly upon the peculiar properties of their protoplasm.—WM. CROCKER.

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[30] RABE, FRANZ, Ueber die Austrocknungsfähigkeit gekeimter Samen und Sporen Flora **95**:253–324. 1905.

Anatomy of Cyperaceae.—The comparative anatomy of the Cyperaceae has been studied by PLOWMAN,[31] and as usual the chief interest centers in the stem. Amphivasal bundles are found throughout the rhizomes of all large-leaved species and at the nodes of aerial stems; elsewhere the bundles are collateral. The amphivasal bundles arise through the introduction into the node of the numerous leaf-trace bundles, and are independent of the branching of the stem. Hence the leaf is to be regarded as the dominant factor in the development of the stelar characteristics of the family and probably of the other monocotyledonous families. The course of the bundles in the rhizome approaches the "palm type," but in the culm the leaf-trace bundles pass down as cortical bundles through one internode and then fuse with the bundles of the central cylinder by a ring-like amphivasal plexus. The seedling and in some cases the floral axis show a simple tubular stele, which is to be regarded as the primitive condition, in contrast with the medullary and amphivasal bundles occurring in many parts of the plant. A cambium is present in the bundles at the nodes of *Scirpus cyperinus* and other species. These features indicate that the Cyperaceae is one of the more primitive groups of monocotyledons, though showing signs of specialization and reduction, accompanied by a high degree of anatomical unity. The view which derives the monocotyledons from an essentially dicotyledonous ancestry receives further support. The author proposes a division of the family into "Amphivasae" and "Centrivasae;" he also gives a key to the genera, based on anatomical characters. The paper is accompanied by a number of excellent photomicrographs.—M. A. CHRYSLER.

Origin of Cycadaceae.—WORSDELL[32] has published a *résumé* of his views as to the origin of the Cycads from the Pteridosperms, with full bibliography. The part dealing with the origin of axial structures is of greatest interest; and the thesis is that the Medullosan ancestry is clear. It is claimed that the cotyledonary node and the axis of the strobilus are the two principal regions for revealing ancestral characters. Much stress is laid upon MATTE'S discovery of polystely in the cotyledonary node of *Encephalartos Barteri;* and also upon the very irregular orientation of the bundles of the peduncle of Stangeria. According to the author's view, the endarch cylinder of Lyginondedron and of the Cycads is of polystelic origin, coming from Medullosan ancestors, each constituent bundle being the homologue of the single bundle of the monostelic Heterangium. The endarch condition arises from the degeneration of the internal vascular tissues. Numerous illustrations are given, intended to show how the various vascular structures of both Pteridosperms and Cycads suggest this view and are most easily explained by it. The whole presentation is

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[31] PLOWMAN, A. B., The comparative anatomy and phylogeny of the Cyperaceae. Annals of Botany. **20**:1–33. *pls. 1–2.* 1906.

[32] WORDSELL, W. C., The structure and origin of the Cycadaceae. Annals of Botany **20**:129–159. *figs. 17.* 1906.

particularly valuable in bringing scattered data together in compact form, although opinions may vary as to their interpretation.

A new term of classification is introduced with "Cycadophyta," used to include Pteridosperms (Cycadofilices), Bennettitales, and Cycadales. The author also discredits somewhat the value of the ontogeny of the vascular structures as indicating their phylogeny.—J. M. C.

Osmosis and osmotic pressure.—A revolutionary paper upon the nature of osmosis and osmotic pressure has been published by KAHLENBERG,[33] who gives detailed accounts of his experiments. He shows clearly that whether osmosis will take place or not depends upon the specific relations between the septum and the liquids bathing it. If osmosis occurs these relations determine the magnitude of the pressure and the direction of the main current. There is, he claims, no such thing as a strictly semipermeable membrane, since a minor movement in the reverse direction always occurs, though it is often insignificant or practically negligible. The force concerned in osmotic processes lies not merely in the specific affinities between the solvent and the solutes, but primarily in their relation to the membrane, whether it be called "potential energy of solution," "internal pressure," or (as KAHLENBERG prefers) "chemical affinity." In measuring osmotic pressures (for which he devised a new apparatus), stirring the liquids is absolutely essential—a factor not previously reckoned with; and in his experiments these measurements show such unlike pressures with the same substances when different membranes are used, and such changes with different temperatures that he holds them irreconcilable with the theory that, as a general rule, solutes conform to the behavior of gases, however closely some in water may do this. The paper deserves the closest attention from every physiologist; yet the weighty evidence against KAHLENBERG'S conclusions must not be forgotten.—C. R. B.

The vitality of buried seeds.—DUVEL gives a preliminary account of experiments on the vitality of buried seeds,[34] of some of the common economic plants and weeds of the United States, representing 109 species, 84 genera, and 34 families. In December, 1902, eight to twelve lots of each species of seeds were buried at three depths: 15–20, 46–56, 90–105$^{\text{cm}}$. A sample of each is to be taken up at given periods and tested for vitality along with controls stored in a dry place.

Tests up to date show the following results. In some cases none of either the controls on the buried seeds grow. Among these are: *Axyris amaranthroides, Bursa bursa-pastoris, Polygonum pennsylvanicum, P. persicaria, P. scandens.*

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[33] KAHLENBERG. L., On the nature of the process of osmosis and osmotic pressure, with observations concerning dialysis. Journ. Phys. Chem. **10**:141–209. 1906. Published also in Trans. Wis. Acad. **15**:209–272. 1906.

[34] DUVEL, J. W. T., Vitality of buried seeds. Bureau Plant Industry Bull. 83. pp. 22. *pls. 3.* 1905.

A second group, among which are the common cereals and various other plants, as *Lactuca sativa*, *Helianthus annuus*, *Asparagus officinalis*, *Pinus virginiana*, *Robinia pseudacacia*, either all decayed before germinating or germinated and then all decayed before being examined. A third group, which includes our more noxious weeds, retained their vitality to a considerable degree. The deeper the seeds were buried the better they retained their vitality. Vitality is best preserved, even in weed seeds, when they are carefully harvested and stored in a dry and comparatively cool place.—WM. CROCKER.

Prothallia and sporelings of Botrychium.—BRUCHMANN[35] has been investigating *Botrychium Lunaria*. Since this species has no means of vegetative multiplication, like the adventitious shoots of *Ophioglossum vulgatum*, every sporophyte must have come from a gametophyte. The prothallia are hard to find because they are very small (1–2^{mm} long and 0.5–1^{mm} wide), and the sporelings grow for several years before they reach the surface of the soil. The prothallia are found at a depth of 1–3^{cm}. In form and general character the prothallium of *B. Lunaria* resembles that of *B. virginianum*, except that it is much smaller. BRUCHMANN succeeded in germinating the spores and his results agree with those of CAMPBELL, who got the two and three-cell stage in *Ophioglossum vulgatum*. Further work upon this aspect of the problem will be published later. However, he represents a single cell at the "spore pole" of the prothallium and regards this as the first cell of the prothallium, representing the protonema stage. Nearly every prothallium bears an embryo and some prothallia have two. The first division of the embryo is transverse. Growth is very slow, the sporeling being three years old before it reaches the surface. One plate and considerable attention in the text is devoted to the anatomy of the mature plant.—CHARLES J. CHAMBERLAIN.

Spermatozoids of Cycas revoluta.—MIYAKE[36] studied the living spermatozoids at the island of Oshima (28° 30′ N) in September, and in southern Japan (31° 35 N) from the beginning to the middle of October. The diameter of the spermatozoids varies from 180 to 210 μ. The two spermatozoids are surrounded by a delicate membrane, but it could not be determined with certainty whether the membrane belongs to the spermatozoid or is merely the *Hautschicht* of the protoplasm of the pollen tube. For observing the movements the spermatozoids were placed in a 10 per cent. cane sugar solution. The movements often continued for one to three hours; and in one case for six hours and forty minutes, and in another case for five hours and thirty minutes. In some cases the spermatozoids were shot out suddenly from the pollen tube, which seems to be the method that occurs under natural conditions. The forward movement is always accompanied by a rotation from left to right about the

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[35] BRUCHMANN, H., Ueber das Prothallium und die Sporenpflanze von *Botrychium Lunaria* Sw. Flora **96**: 203–230. *pls. 1–2.* 1906.

[36] MIYAKE, Ueber die Spermatozoiden von *Cycas revoluta*. Ber. Deutsch. Bot. Gesell. **24**: 78–83. *pl. 6.* 1906.

axis. In some cases the forward movement was found to be at the rate of 0.7^{mm} per second. MIYAKE agrees with WEBBER that the liquid in the archegonial chamber at the time of fertilization comes from the pollen tube and not from the archegonium.—CHARLES J. CHAMBERLAIN.

Heterostyly and gynodioecism.—Inheritance of dimorphism has been investigated by RAUNKIÄR[37] in Primula, Menyanthes, Pulmonaria, Fagopyrum, Knautia, and Thymus. In all heterostylic species studied he finds that the long-styled and short-styled forms occur in about equal numbers regardless of the character of the environment. In gynodioecious species, on the other hand, he finds considerable variation in the proportions of the two forms in different localities. The results of breeding are in close accord with those of CORRENS,[38] except in an interesting case in which a cross between two bisporangiate plants of *Thymus vulgaris* produced 65 per cent. pistillate plants. In *Primula officinalis*, brachystylic plants pollinated by brachystylic produced 62.5 per cent. brachystylic, brachystylic × dolichostylic gave 55.2 per cent. brachystylic, and dolichostylic × dolichostylic only 4.3 per cent. brachystylic. Investigation covering several generations is needed to determine the effects of the pre-parental ancestry, and until this is done, any speculation as to the hereditary nature of the forms of a dimorphic species can be of little value.—GEORGE H. SHULL.

Development of spores of Helminthostachys.—BEER[39] has investigated the development of the spores of H. *zeylanica*, his material being fertile spikes preserved in spirit. CARDIFF,[40] and afterwards STEVENS,[41] had described the peculiar blocking out of the sporogenous tissue and the remarkable behavior of the plasmodium-like tapetal cytoplasm in Botrychium; and BEER finds the same phenomena in Helminthostachys. His observations extend, however, to the specific work of the tapetal plasmodium in spore-formation. The observed facts are that during the period of exospore growth the tapetal plasmodium shows more or less complete disappearance of starch, gradual diminution of the finely vacuolar cytoplasm, and richly chromatic nuclei which often show irregularities of outline. The conclusion is that the tapetal plasmodium is the center of metabolic activities in which a substance is elaborated from the raw materials contained in the tapetum, and is employed, directly or indirectly, in the growth of the spore wall.—J. M. C.

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[37] RAUNKIÄR, C., Sur la transmission par hérédité dans les espèces hétéromorphes. Bull. Acad. Roy. Sci. et Let., Denmark, pp. 31–39, 1906.

[38] See BOT. GAZETTE **39**: 304. 1905. and **41**: 302. 1906.

[39] BEER, RUDOLF, On the development of the spores of *Helminthostachys zeylanica*. Annals of Botany **20**: 177–186. *pls. 11–12.* 1906.

[40] BOT. GAZETTE **29**: 340–347. *pl. 9.* 1905.

[41] Annals of Botany **19**: —. —. 1905.

Seedlings of Piperales.—In continuing his work on the structure of the seedlings of certain Piperales, HILL[42] has published results dealing chiefly with several species of Peperomia. The transition phenomena are described in detail; that is (in brief), the arrangement of the vascular tissues in the cotyledonary or primary node, the transition region between root and stem, where the earliest tissues of the vascular system arise. The conclusion in reference to the primitive or reduced character of Peperomia is confirmatory of JOHNSON's view that it is a reduced genus, the determining factor in reduction possibly being the epiphytic habit of many forms. It is also suggested that these transition phenomena may not be such important phylogenetic criteria as has been assumed by some investigators, since they do not seem to be sufficiently rigid to withstand the influence of varying conditions.—J. M. C.

Antipodal cells.—In a long article LOTSCHER[43] discusses the structure and function of the antipodal cells of angiosperms. On the basis of their anatomy and physiology he finds three types of antipodals: (1) those remaining as naked protoplasts or free cells and functioning in the resorption of the nucellus (Orchidaceae, Cruciferae, Geraniaceae, Linaceae, Papilionaceae, Primulaceae, Polemoniaceae, and Scrophulariaceae); (2) those well differentiated and forming a roundish cell-complex which serves to transform the foodstuffs which are brought to the embryo-sac (Gramineae, Araceae, Ranunculaceae, Mimosaceae, Cesalpinaceae, and in combination with the third type, predominant in Liliaceae, Iridaceae, Zingiberaceae, Borraginaceae, and Solanaceae); (3) those, singly or together, having an elongated form and functioning principally as haustoria (most Rubiaceae).—CHARLES J. CHAMBERLAIN.

Mechanics of secretion.—This problem has been attacked by LEPESCHKIN, who finds[44] that from "unicellular" plants (Pilobolus, Mucor, Phycomyces, and Vaucheria are so called), as well as from the epidermal structures of green plants, secretion is to be referred to the unlike permeability for solutes of the plasma membrane in the absorbing and secreting regions of the structure. The process of secretion and the influence of external agents upon it agree completely with the mathematical formulae for the energy involved, based upon the current theories of osmotic pressure. The permeability of the membrane is easily altered by external and internal influences. Whether this is characteristic of all semipermeable membranes or only of plasmatic membranes remains to be determined. The research adds some facts but leaves much yet to be explained regarding the subject.—C. R. B.

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[42] HILL, T. G., On the seedling-structure of certain Piperales. Annals of Botany **20**:160–175. *pl. 10.* 1906.

[43] LOTSCHER, P. KONRAD, Ueber den Bau und die Funktion der Antipoden in der Angiospermen-Samenanlage. Flora **94**:213–262. *pls. 1–2.* 1905.

[44] LEPESCHKIN, W. W., Zur Kenntniss des Mechanismus der aktiven Wasserausscheidung der Pflanzen. Beihefte Bot. Cent. **19**:409–452. 1906.

Pollen grains of Picea.—POLLOCK[45] has described variations observed in the pollen grain structures of *Picea excelsa*, chiefly in reference to the so-called prothallial cells. The usual number of these cells reported for the Abietineae is two, but POLLOCK finds the variation in Picea to range from one to three, with one as the number in the majority of cases. This is an interesting situation, as these cells have been reported thus far for the conifers only among the more primitive Abietineae and Podocarpeae, and it shows that even here they are in a very fluctuating condition. The condition among the Araucarias, recently announced by THOMSON, is interpreted as representing a still greater multiplication of prothallial cells, an interpretation that is probably justified. That among the conifers all stages in the elimination of this tissue are represented seems evident.—J. M. C.

Sclerotinia on Forsythia.—OSTERWALDER[46] has described a disease of species of Forsythia induced by *Sclerotinia Libertiana* which has heretofore been reported only upon herbaceous plants. The fungus infects the shoots of Forsythia only through the withering flowers, and extends up and down the woody branches from those points, causing a wilting of the twigs alone. Sclerotia are formed abundantly on the infected parts and after being kept over winter produce the typical apothecia of Sclerotinia. Spores or mycelium grown therefrom produced the disease anew when placed on the floral parts. Although Botrytis conidiophores occurred on some of the withered flowers, the author was able to show that these were not connected with the Sclerotinia, thereby supporting the view that *Sclerotinia Libertiana* has no conidial form.—H. HASSELBRING.

A sterile Bryonia hybrid.—In studying the development of the sex organs of a sterile hybrid of *Bryonia alba* and *B. dioica*, TISCHLER[47] comes to the conclusions that the absolute sterility has nothing to do with the tetrad formation because the megaspore series shows the normal tetrads, and that while there are irregularities in the formation of pollen there are also cases in which normal pollen is formed. It is possible that the cause of sterility in hybrids is more complicated than has been supposed. This work does not support the theory that sterility is due to total or partial loss of power by the male or female chromosomes. It may be that the sterility is due to a low nutrition of the protoplasm. It seems probable that the cause of sterility can best be investigated by combining culture methods and cytology.—CHARLES J. CHAMBERLAIN.

Photosynthesis.—USHER and PRIESTLEY have contributed strong support to the theory of BAEYER that formaldehyde is the first product of photolysis of CO_2.

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[45] POLLOCK, JAMES B., Variations in the pollen grain of *Picea excelsa*. Amer. Nat. **40**:253–286. *pl. 1.* 1906.

[46] OSTERWALDER, A., Die Sclerotienkrankheit bei den Forsythien. Zeitsch. Pflanzenkr. **15**:321–329. *pl 5.* 1905.

[47] TISCHLER, G., Ueber die Entwicklung der Sexualorgane bei einem sterilen Bryonia-Bastard. Ber. Deutsch. Bot. Gesell. **24**:83–96. *pl. 7.* 1906.

They find[48] an enzyme in spermatophytes and pteridophytes generally, which decomposes H_2O_2 energetically, with the evolution of O_2. When this enzyme is destroyed or its action inhibited, the chlorophyll is quickly destroyed and the plant bleached. They also demonstrated the formation of formaldehyde (when its prompt condensation was prevented) in the immediate vicinity of the chloroplasts. The usual condensation of the HCOH is due, they hold, to the protoplasmic stroma of the chloroplast and not to an enzyme; yet the experiment on which they rely is not conclusive on this point.—C. R. B.

Seeds of Euphorbiaceae.—A study of the development of the seeds of numerous genera and species of Euphorbiaceae has given SCHWEIGER[49] the following results: The obturator, a tissue which serves for the conduction and nutrition of the pollen tube, is always present. It disappears gradually after fertilization, leaving only a slight remnant which belongs to the placenta and never to the seed. The tip of the nucellus is often much elongated, and until fertilization is effected is often in direct connection with the obturator. The caruncle belongs to the seed, is developed from the outer integument, and serves to separate the seed from the placenta.—CHARLES J. CHAMBERLAIN.

Zygospores of Mucor.—According to HAMAKER[50] the production of zygospores of *Mucor stolonifer*, with proper conditions of moisture and temperature, is dependent only upon the nature of the substratum. The atmosphere should be saturated with moisture and the temperature about 70° F. The substratum used is corn muffin bread, which the baker makes after the following formula: corn meal, 16 pounds; flour, 3 pounds; lard, 3 pounds; salt, ½ pound; eggs, 48; sweet milk, 3 gallons; baking powder, 18 ounces. In a large proportion of cultures zygospores appear in five to seven days.—CHARLES J. CHAMBERLAIN.

Germination of pollen.—JOST has succeeded in germinating the pollen grains of various grasses,[51] which have heretofore proved refractory, by growing them under conditions where they can obtain water very slowly from the medium by which it is held. Thus, a starch paste made with only one or two parts of water proved useful; and also parchment paper soaked with a sugar solution. The pollen grains of certain Compositae have also yielded to the latter treatment, but none of the Cichoriaceae or Umbelliferae.—C. R. B.

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[48] USHER, F. L., and PRIESTLEY, J. H., A study of the mechanism of carbon assimilation in green plants. Proc. Roy. Soc. London B. **77**:369–376. 1906.

[49] SCHWEIGER, JOSEPH, Beiträge zur Kenntniss der Samenentwickelung der Euphorbiaceen. Flora **94**:339–379. 1905.

[50] HAMAKER, J. I., A culture medium for the zygospores of *Mucor stolonifer*. Science N. S. **23**:710. 1906.

[51] JOST, L., Zur Physiologie des Pollens. Ber. Deutsch. Bot. Gesells. **23**:504–515. 1906.

Dry rot.—BULLER[52] describes the destruction of pine paving blocks in Birmingham, England, by *Lentinus lepideus* Fr. This fungus produces a dry rot which in its microscopic and chemical aspects resembles the destruction of wood by *Merulius lachrymans*. Cellulose is removed from the walls and hadromal is left behind. The ravages of the fungus were somewhat checked by a dipping in creosote which the blocks had received before being laid down. —H. HASSELBRING.

Self-digestion of endosperm.—POND summarizes[53] the literature on this point, and finds no clear proof that the amylaceous endosperm of grasses or the horny endosperm of palms is capable of self-digestion, though this has been claimed by authors and the claim has been accepted hitherto. He himself carefully tested this point in the seed of the date, *Phoenix dactylifera*, and finds its endosperm incapable of self-digestion.—C. R. B.

Formation of chlorophyll.—According to PALLADIN this is a process of oxidation, dependent upon the presence of sugar solutions of low concentration (10%); but ISSATCHENKO reports[54] that chlorophyll formation depends only on the energy of light, occurs in conditions deemed unfavorable by PALLADIN, and is not inhibited by concentrations of even 30–50 per cent. sugar in detached leaves of *Vicia Faba*.—C. R. B.

Caprification.—LONGO has been investigating the fig and caprifig, and in advance of the full memoir with illustrations has published a brief preliminary announcement.[55] As the differences from previous accounts are those of detail rather than fundamental in character, a review will be deferred until the appearance of the full paper.—J. M. C.

Anatomy of Epigaea.—The histology of the stem and leaf are described in a paper by ANDREWS.[56] The most noteworthy point is the occurrence of glandular hairs on the lateral branches, and the suggestion is made that these aid in absorption of food.—M. A. CHRYSLER.

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[52] BULLER, A. H. REGINALD, The destruction of wooden paving blocks by the fungus *Lentinus lepideus* Fr. Jour. Economic Biol. **1**:1–12. *pls 1–2.* 1905.

[53] POND, R. H., The incapacity of the date endosperm for self-digestion. Annals of Bot. **20**:61–78. 1906.

[54] ISSATCHENKO, B., Sur les conditions de la formation de chlorophylle. Résumé. Bull. Jard. Imp. Bot. St. Petersb. **6**:27. 1906.

[55] LONGO, B., Ricerche sul fico e sul caprifico. Rend. Accad. Lincei **15**:373–377. 1906.

[56] ANDREWS, F. M., Die Anatomie von *Epigaea repens* L. Beih. Bot. Cent. **19**: 314–320 *pls. 6–8.* 1905.

NEWS.

Dr. W. W. Rowlee, Cornell University, has been advanced to a full professorship of botany.

Dr. C. F. Hegelmaier, professor of botany at the University of Tübingen, has died at the age of 72 years.

Professor L. M. Underwood, Columbia University, has received the degree of doctor of laws from Syracuse University.

Dr. Franz Buchenau, the well-known monographer of Junaceae, died at Bremen, April 23, at the age of seventy-five years.

The German Botanical Society has offered a prize of 1000 marks for a monograph on polymorphism in the algae.—Science.

Dr. D. T. MacDougal has been elected a foreign member of Hollandsche Matschappij van Wetenschappen, the Dutch Academy of Sciences.

Professor Bruce Fink, the lichenologist, of Iowa College, has resigned to accept a professorship of biology in Miami University, Oxford, Ohio.

Dr. Friedrich Czapek, of Prague, has been appointed professor of botany and director of the botanic garden and institute of the University of Czernowitz.

Professor George Macloskie, Princeton University, has retired from active service, having been appointed Professor Emeritus. He has been in charge of the botany of that institution since 1875.

Botanical appointments confirmed recently by the trustees of the Ohio State University are as follows: Robert F. Griggs, assistant professor; Freda Detmers, instructor; and L. A. Hawkins, fellow.

Professor Conway MacMillan has resigned the professorship of botany at the University of Minnesota and will devote his attention to business. The position is to be filled by promotion from the present staff.

Professor D. H. Scott's presidential address before the Royal Microscopical Society, entitled "Life and Work of Bernard Renault," is published in Jour. Roy. Micr. Soc. **1906**: 129–145, with an excellent portrait.

Howard S. Reed, instructor in botany at the University of Missouri, has resigned his position to accept an appointment in the Bureau of Soils, United States Department of Agriculture. H. L. Shantz has been appointed to succeed him.

THE EIGHTH annual session of the biological station of the University of Montana will be held at Flathead Lake from July 11 to August 16. This station combines the advantages of lake, plain, and mountain. Botany is in charge of THOMAS A. BONSER, of the Spokane high school.

HIS ASSOCIATES on the faculty of Brown University lately presented to Professor W. WHITMAN BAILEY a loving-cup, in token of their esteem for him personally and in commemoration of his twenty-nine years of active service, from which he retires this year. At a meeting of the trustees at Commencement he was appointed Professor Emeritus.

MRS. J. H. SCHAFFNER, of Columbus, Ohio, died recently after a brief illness. This is not only a sad loss of a devoted companion to Professor SCHAFFNER, but a botanist of promise and ability has passed away. Mrs. SCHAFFNER had published little, perhaps only one paper, over her own name, but a piece of completed cytological work will soon appear as a posthumous paper.

IN THE *Generalversammlungs-Heft* closing volume 23 of *Ber. Deutsch. Bot. Gesells.*, the following biographical sketches are published: WILHELM SCHWACKE, by TH. LOESENER; EDUARD TANGL, by G. HABERLANDT; JOHANN ANTON SCHMIDT, by E. PFITZER; OTTO WÜNSCHE, by J. ABROMEIT; FEDERICO DELPINO, by O. PENZIG; LÉO ERRERA (with portrait), by E. DE WILDEMAN.

AT THE REQUEST of some members of the American Medical Association Dr. HERMANN VON SCHRENK made a pathological exhibit at the recent meeting of this association in Boston. The exhibit showed types of some diseases of plants and some of the conditions producing these diseases. The manner of infection and spread of disease, the symptoms and causes, the methods of treatment and of investigation were illustrated. The time for securing the material was extremely limited, but nevertheless the exhibit occasioned much surprise to the medical men, though it showed but partially the work which plant pathologists have accomplished.

ERRATUM.—The date of publication of the June number was incorrectly given in the table of contents for the month, and in the list of dates of publication accompanying the title pages of the volume. On p. vi, line 23, for June 30 read July 7.

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No. 2

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August, 1906

Editors: JOHN M. COULTER and CHARLES R. BARNES

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Vol. XLII, No. 2 Issued August 30, 1906

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BRIEFER ARTICLES.

CURRENT LITERATURE.

Communications for the Editors should be addressed to them at the University of Chicago, Chicago, Ill.

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AUGUST, 1906

THE NASCENT FOREST OF THE MISCOU BEACH PLAIN.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 4.[1]

W. F. GANONG.

(WITH FOURTEEN FIGURES)

THE extreme northeastern angle of the Province of New Brunswick, as the accompanying map will show, is formed by the island of Miscou. The northwestern margin of this island is an extensive sandy beach plain, growing rapidly by action of the sea, locally called Grande Plaine. On this plain there is developing a forest which exhibits every stage of formation from the salt plants of the open sea beach to the heterogeneous vegetation of the mixed woods. The conditions are unusual and the phenomena of proportional interest. In August 1905 I was able to give the place some two weeks of observational study, with results which follow.

In all such studies as this the correct identification of the plants is of first importance, and identification is becoming a matter of such difficulty that only a professional systematist is competent authority. Accordingly I have sent all of my collections, including a specimen of every plant I found at Grande Plaine, to Professor M. L. FERNALD, of the Gray Herbarium of Harvard University, who has been so kind as to determine their identity, and, as well, to give me the names they should bear in accordance with the recommendations of the Vienna Congress. I wish here to express my indebtedness to him and my best thanks for this invaluable aid. Such is the origin of the nomenclature of this paper.

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[1] No. 3 is in the BOT. GAZETTE **36**:161–186, 280–302, 349–367, 429–455. 1903.

As to previous literature of this particular subject, there is none. In 1886 Dr. G. U. HAY made a collection of Miscou plants for the Geological Survey of Canada, but no account of them was ever published, and no other botanist has heretofore been on the island. In many respects, however, as the reader will observe, the vegetation of this beach plain resembles closely the vegetation of the sand beaches and dunes of Lake Michigan as described in COWLES's well-known memoir,[2] and many of the conclusions of that work are also applicable here.

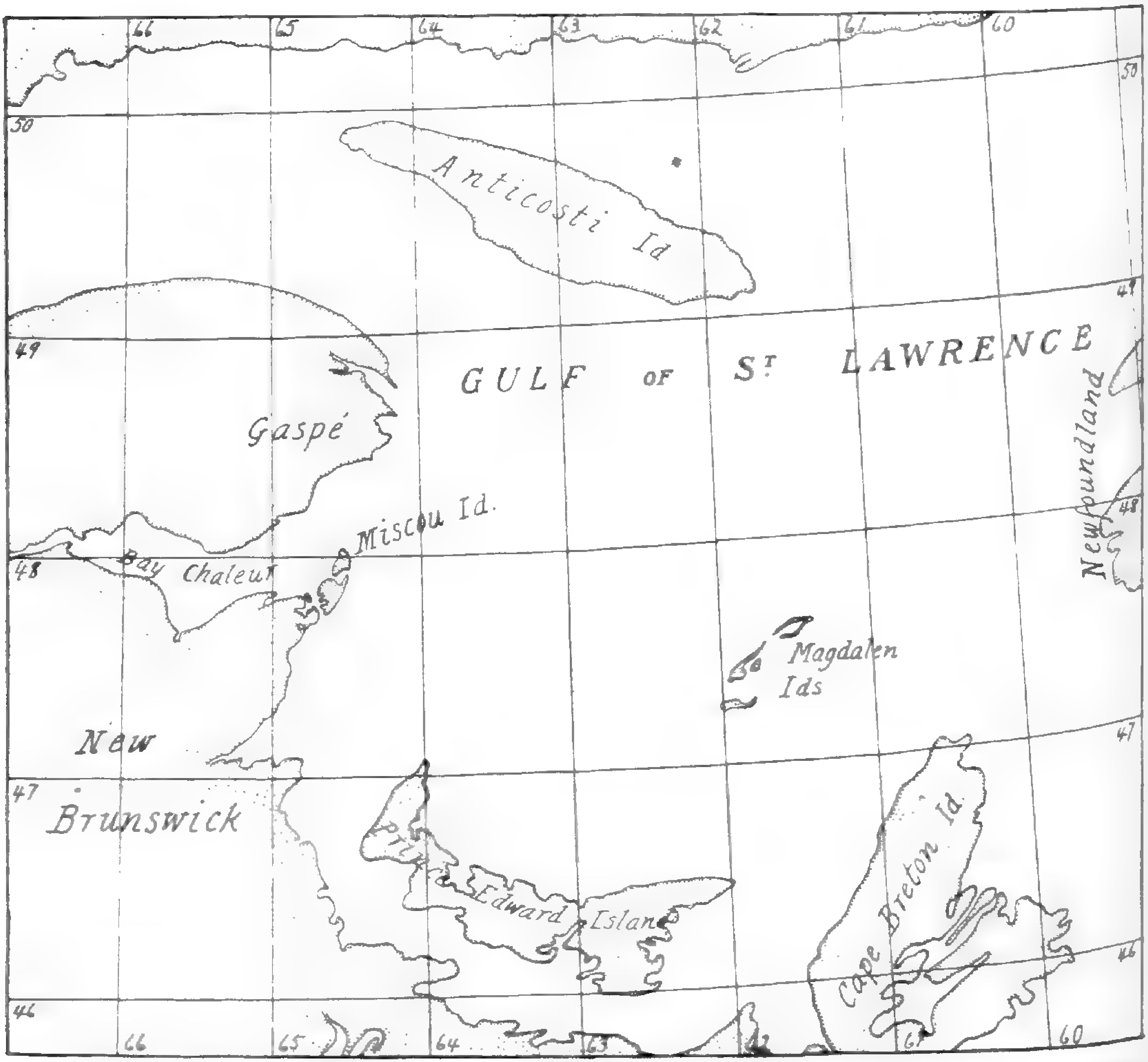

FIG. 1.—Outline map of part of the Gulf of St. Lawrence, to show the geographical position of Miscou Island.

Grande Plaine extends along the west side of Miscou. Beginning on the south at Eel Brook (see the accompanying map, *fig. 2*),

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[2] BOT. GAZETTE **27**:95–117, 167–202, 281–308, 361–391. 1899.

where it is but a few yards wide, it rapidly broadens northward until it reaches some half a mile across, and then narrows again towards its northern end, which is also the northernmost point of the island. Though nearly level as a whole, it is by no means flat, for it is composed of a series of approximately concentric dune beaches, which, two or three in number at Eel Brook, increase to over forty opposite Lac Frye. In height these dune beaches vary from two to five or six or even seven feet (0.6–2^{m}) and in breadth from eight or ten up to forty or fifty paces. At its widest part, which comprises some thirty or more of the beaches, new ones are plainly being rapidly added, while at its northern end the entire plain is being washed away by the sea, which is cutting sharply across the ends of the old beaches. About two-fifths of the plain, including the older parts next the upland, are forested; about two-fifths, including all the outer and newer parts, are open, clothed only by the waving beach grass; the intermediate zone, a small one-fifth of the area of the plain, is a

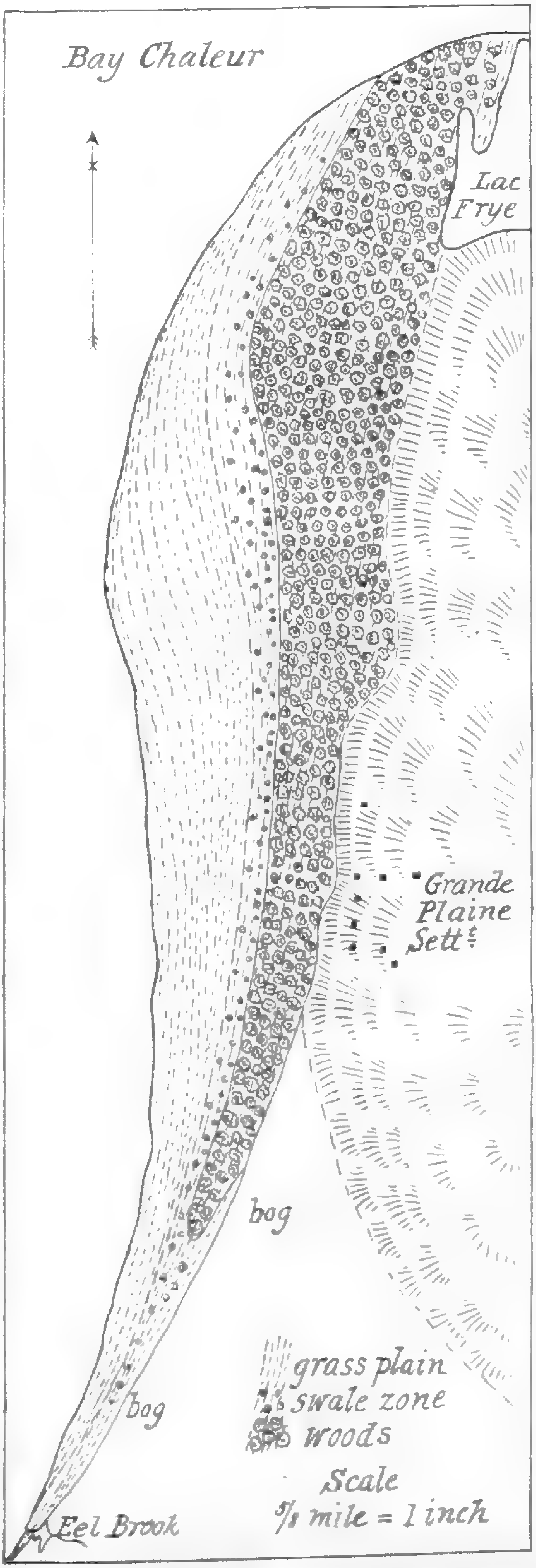

Fig. 2.— Map of Grande Plaine, Miscou Island; from an amateur survey by the author; dotted boundaries are only approximate; the heavier dotted line outside the swales represents approximately a line of higher dune beaches.

transition zone where the forest is pushing its advance into the open ground. The mode of formation of this remarkable plain, involving the anomaly of extensive land-building on a sinking coast, I have described somewhat fully elsewhere.[3] Briefly, the facts are these. As the result of peculiarities of the topography, wind, and tides of this region, there is formed on the shallow northwestern side of Miscou a kind of great eddy in which all movable materials, sand and gravel from the wear of the rapidly crumbling adjacent coasts, as well as driftwood, waterweeds, and other flotsam, often from a great distance, tend to collect, and thence are driven ashore by the prevailing westerly winds. Formerly the island extended farther north than now, carrying with it both eddy and plain; but the general subsidence actively in progress in this region has carried its low northerly end beneath the sea, thus forcing the eddy and the accompanying plain-building gradually southward. The northern end of Grande Plaine today is being rapidly washed away (compare map), to be redeposited farther south, and the plain as a whole is thus rolling by its outer margin southward along the coast. The subsidence of the land has produced another effect upon the plain, and one of considerable consequence to its vegetation, namely, its inner and older part averages somewhat lower, that is, less above sea-level, than the outer and newer part, thus leading to a settling of water towards the older inner parts, and a relatively higher water-table in them. That we have here a beach plain, instead of a series of lofty sand dunes, is the result of the fact, apparently, that the dry sand of the beach is blown ashore no faster than the beach grass can fix it. At both the northern and southern ends of the plain, however, there is some approach to a building of true, though low, dunes.

My brief study of the vegetation of Grande Plaine was entirely observational, not at all instrumental, nor do any meteorological or other exact physical data for this region exist. Grande Plaine lies at sea-level in latitude 48°, beside a shallow sea, warm in summer but frozen over in winter. The summer climate is remarkably equable, of a temperature most comfortable for man, with no fogs and but little cloudy weather. The rainfall must be not far from

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[3] Bull. Nat. Hist. Soc. N. B. No. 24:453. 1906.

45 inches. Heavy winds from the west prevail in summer. The soil is of pure quartz sand derived from the wear of the gray carboniferous sandstones of the region, this sand having, of course, the usual relations to water-supply, mineral nutrients, etc. No other special factors with a bearing upon the vegetation appear to be prominent.

We turn now to consider the vegetation. Although it presents every gradation from humble herbs of the open beach to the densest woods, nevertheless the eye becomes accustomed to recognize, and the speech to designate, certain definite vegetational regions. These represent the modes or climaxes, as it were, in the vegetation curve —the parts which exhibit a distinctive character in the physiognomy of the whole. They are the following: (1) the new beach, (2) the grass plain, (3) the swales, (4) the sandy woods, (5) the closed woods.

THE NEW BEACH.

The characteristic open, or new, beach of Grande Plaine, the kind which best illustrates the mode of growth of the plain, is to be found opposite its middle and broadest part; for towards the northern and southern ends its structure is modified by local conditions of erosion and dune-building. Outside of all is a broad sloping inter-tidal beach of pure sand without vegetation (*fig. 3*). Above it is the narrow band between ordinary and extreme high tides, from which the drying sand is being driven landward by the winds; it is also vegetationless, or with but stragglers from the upper beach. Finally, there is that broad shelf, very well shown in the accompanying photograph (*fig. 4*), reached only by the very highest tides, composed of fine quartz sand, intermixed with some gravel and occasional flat cobbles; it is covered with scattered driftwood among and over which the dry sand is being forever driven, shifted, and piled. Thus the new beach offers a barren habitat to plants, for it has a mineral-poor soil, drenched often by salt, forever shifting, and exposed to the unbroken force of frequent heavy winds. The vegetation is plainly responsive to these conditions. It is extremely scanty, the plants growing widely isolated, while many square yards do not show any vegetation at all. Thus competition among the plants seems not to exist, and the struggle is wholly with the physical environment. The most characteristic plant by far is the small, radiate-decumbent, succulent, annual saltwort, *Salsola Kali*, which occurs but rarely and for the most part in the lee of

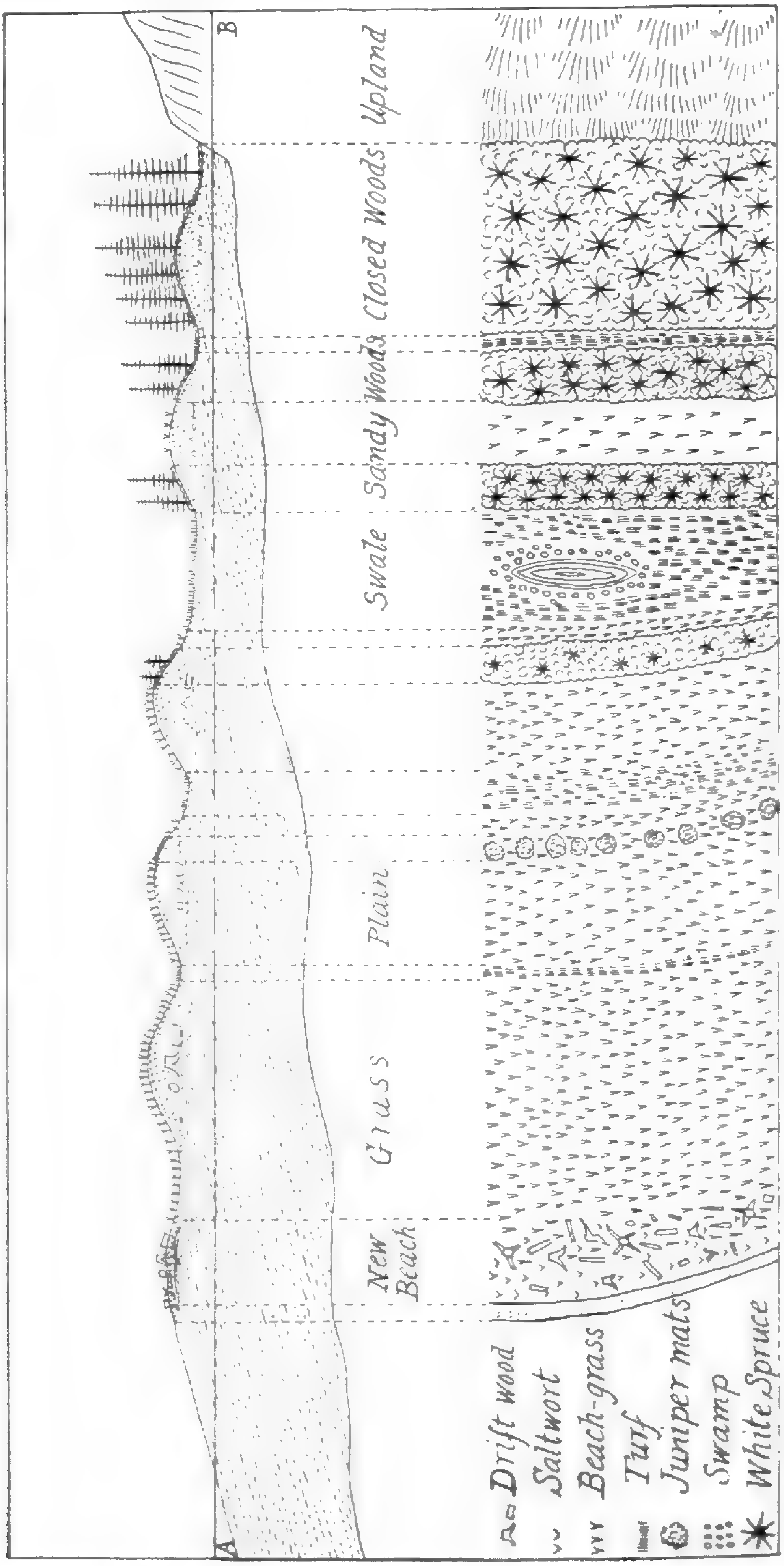

FIG. 3. Idealized section and map to show the mode of formation of the beach plain, and the distribution of its vegetation; the line *AB* is true level, and may be taken to represent approximately the position of the water-table.

some shelter, such as a hollow or large piece of driftwood. Next in abundance, though but scarce, is the little fleshy, rosette-like, annual sea rocket, *Cakile edentula* (*C. americana*). Third in abundance is the low halo-rosette, perennial sea lungwort, *Mertensia maritima*, here seemingly growing as an annual, also mostly in places of some shelter. Rarely, and then only in a sheltered position, occur tiny radiate-creeping plants of the beach pea, *Lathyrus maritimus*, growing apparently only as an annual, and sometimes showing a marked difference in the windward-creeping and leeward-creeping shoots on the same plant, the former being much shorter and smaller-leaved. Even rarer is the radiate-creeping, small-leaved, halo-scurfy annual, *Atriplex patula hastata*. Here and there, however, especially in sheltered places, arise the tufted culms of the beach grass, *Ammophila arenaria*, the characteristic sand-binding perennial of the dune beaches next to be considered, here seemingly growing from seed. I was able to find no other plants on the new beach. Thus we see that this vegetation is distinctly adjusted to the physical conditions, for it is of great paucity, of small and slow growth, annually renewed, closely ground-appressed, and strongly xerophytic.

FIG. 4.—Typical open, or new, beach, looking north; among the driftwood occur scattered tufts of saltwort and beach grass.

THE GRASS PLAIN.

Inside the line of open beach begins the sand plain, composed of a great number of approximately parallel dune beaches, forming smoothly swelling ridges and hollows of elevations and breadths already described. Every dune beach, I believe, originates with a core of driftwood. As the tidal beach is built outwards by the addition of sand, driftwood continues to collect on its uppermost part, until finally some unusual combination of great winds with high tides sweeps it up beyond reach of further disturbance. Then the driving sand from the beach is caught among it; the beach grass gains a foothold in the sheltered places, spreads, and checks the further movement of this sand. Then more sand is driven shoreward, and it grows into a low dune which is fixed by the beach grass as fast as it rises. The limit is reached only when a new line of driftwood has been formed outside and begins to stop the sand for its own growth. The resultant dune beach offers severe conditions for plant life, for its surface is swept, especially on the summit and windward slope, by heavy winds; it is heated intensely by the sun; it is readily movable; and it forms a soil extremely poor in mineral nutrients.[4] It lacks the salt of the newer beaches, however, for this is soon removed by the rain; and it possesses an ample supply of moisture a foot or two beneath the surface, for the supply brought by the rain drains but slowly away, owing to the low gradient of the water-table. These conditions, especially at their extreme on the summits and windward slopes of the beach dunes, are endured by practically but a single plant—the herbaceous-perennial, subterranean-creeping, xero-culmed, deep-rooting beach grass, *Ammophila arenaria,* which occurs, without any competitor whatever, in open scattered tussocks, only partially covering the ground, as well shown in *fig. 5,* and in closer view in *figs. 6* and *7.* It happens that this grass is of considerable economic value to the neighboring farmers, who cut it and haul it for hay, and whose cattle graze upon it; its destruction in this way causes an irregular exposure of the outer beaches, permitting them to be irregularly cut by the wind. It is for this reason, I have no doubt, the newer outer beaches

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[4] As indicated by KEARNEY'S recent studies: BOT. GAZETTE 37:426–436. 1904.

are so much more irregular in their various characters than the older inner beaches, which antedate the advent of man.

But while the beach grass has no competitor, it affords a shelter, especially behind its tussocks, permitting the growth of a number of other plants, which, however, form but an insignificant part of the entire vegetation, and which are widely separated from one another. Most important of these, perhaps, is the beach sedge *Carex silicea*, which grows in scattered tussocks here and there among the beach grass, and it is indeed the only other plant which seems at home in this situation. The remainder of the plants, all sparsely or rarely represented, are obviously stragglers from the most diverse habitats, many of them quite unexpected residents in such a situation. Thus, dwarfed saltwort strays in from the beach, and the beach pea is here somewhat more flourishing than on the open beach. Then there are greatly dwarfed individuals of certain ubiquitous forms able to endure a wide range of physical conditions, such as the dandelion, *Taraxacum officinale*, which extends in sheltered spots even to the outer margin of the plain; the Canada thistle, *Cnicus arvensis;* the sow thistle, *Sonchus arvensis;* the

FIG. 5.—Typical grass plain, looking north; practically no plant visible except the beach grass.

field sorrel, *Rumex Acetosella*, in dwarfed-rosette, very red forms; the evening primrose, *Oenothera biennis;* and the moonwort, *Botrychium ternatum intermedium.* There are also some forms usually characteristic of rather a dry habitat, such as the pearly everlasting, *Anaphalis margaritacea*, and a western yarrow, *Achillea lanulosa.* In addition there are others, generally in more sheltered spots and also greatly dwarfed, which usually prefer a moister habitat, such as the two western roses, *Rosa acicularis* (*R. Sayi, R. Engelmanni*) and *Rosa lucida;* a western violet, *Viola adunca;* a stitchwort, *Stellaria longipes laeta;* a silver weed, *Potentilla Anserina concolor;* the stellate false Solomon's seal, *Smilacina stellata;* and one of the vetches, *Vicia Cracca.*[5] The great diversity of natural habit of these plants, their scanty and irregular occurrence, and their dwarfed size and rosette-forming tendency all unite to show that none of them are here at home. Obviously they are the ones which, of all the many kinds which must be brought to this plain by natural modes of dissemination, are sufficiently tolerant physiologically to be able to germinate under, and then to withstand, these extreme physical conditions, eking out here a starved and precarious existence. The conditions for germination upon the sand must be extremely severe, and it is very likely that other kinds of plants could exist here as adults, could their seeds develop; and further it is probable that the individuals which do exist on the plain are those whose seeds happened to fall in especially favorable spots, or became properly buried by the moving sand. Else why are they so few? The universal dwarfing is due in all likelihood not to the heat and dryness of the surface, nor to any salt content in the soil, and certainly not to a scarcity of soil water, but to the paucity of mineral nutrients in the sand. This is in harmony with another feature they mostly show in common—very deep and, I think, much-branching roots. The fact that they come

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[5] The following Grande Plaine plants appear to be new to the flora of New Brunswick: *Achillea lanulosa, Viola adunca, Rosa acicularis, Stellaria longipes laeta,* and *Potentilla Anserina concolor.* Certain others are new in name, the species having been recently more exactly defined and segregated: *Alnus mollis, Myrica carolinensis, Vaccinium Vitis-Idaea minor.* Others are new in name because made to conform to the rules of the Vienna Congress, but in these cases the names of Gray's *Manual*, 6th edition, have been given in brackets.

from such a diversity of natural habitats, and yet live in this peculiar situation upon an equal footing, shows how far we are from understanding the real bases of physiological adaptation, and further shows that in the study of the physiological life-histories of plants lies the most important and attractive field for the ecologist of the near future.

So much for the exposed parts of the dune beaches. But in addition they offer, upon their inner or leeward slopes and in the hollows, situations more sheltered, not so much from the sun, since

FIG. 6.—Typical hollow between outer dune beaches; the tall grass is all beach grass, but the small plants among it are the common strawberry.

their average course is nearly north and south, but from the westerly winds. The older inner dune beaches also are protected to some extent by the newer outer ones, as well as by their slightly lower average level. The difference between leeward slope and hollow is not simply one of degree of shelter, however, but also of physical conditions, for the hollow is much nearer the source of water supply, the free table of which is not over a foot or two beneath the surface. In consequence of these differences we can recognize three distinct phases of vegetation: *first,* a larger development on the leeward slopes of plants which are small and rare on the outer slopes; *second*, a distinctive vegetation of the hollows; and, *third*, a distinctive vegetation of the inner slopes.

As to the first phase, it is enough to note that several plants, in particular the pearly everlasting and the wild roses, small, scarce, and scattered on the outer slopes, become larger, frequent, and even patch-forming on the inner; and this is true also in less degree of other species. The beach grass persists in all situations.

The second phase is the vegetation of the hollows. The very first plant to appear in this situation, and that too near the outer beaches, is always, strangely enough, the common wild strawberry, *Fragaria virginiana*, apparently of normal size and form, seemingly quite at home, and spreading abundantly by runners, so that it forms considerable patches. The appearance of the nascent patches is well shown in *fig. 6*. As soon as the patches reach an appreciable density, such that they afford a cover to the ground, then turf-forming grasses, of which the first is the red fescue, *Festuca rubra*, appear and initiate the turf-formation which is so important a feature of the swales to be described below. The strawberry, of course, is one of the most tolerant, and hence ubiquitous, herbs of our flora, and its situation here is partially explained by the nearness of the abundant water supply. Yet it is surprising to find it taking so important a part in a vegetation in so peculiar a position.

The third phase of this vegetation is that characteristic of the sheltered slopes. First of such plants to appear, and the most common and characteristic, is the dwarf creeping juniper, *Juniperus Sabina procumbens*, of which single plants originate just below the beach dune crests, and creep radiating, more to leeward than to windward, in a close dense mat covering many square feet. A young plant is shown in *fig. 7*, in characteristic form and position. On the inner beaches these plants occur upon the outer as well as the inner slopes, and the shelter of the mats thus formed affords in reality the principal starting-point for the development of other plants which lead gradually to the development of the forest, as will be noted under the transition vegetation. In a similar situation, but independently, arise patches of two other characteristic plants, a bright-green, leathery-leaved, tufted shrub, the wax berry, *Myrica carolinensis*, which comes to form dense discoid (sometimes almost fairy-ring like) masses on the crests and inner slopes; and the less frequent, low, dense-tufted, white-hairy shrub, *Hudsonia tomentosa*, in irregular close patches. All of these plants are pronounced xerophytes, which amply explains their ability to live in this situation, and even their preference for the somewhat drier upper slopes of the dune beaches. Their xerophilism, in common with that of many other evergreen sand plants, is, as I guess it, an adaptation to the physiological dryness which results when, as must often be the case in spring and fall, the ground water is of low temperature and hence slowly absorbed, while the leaves are exposed to high transpiration conditions from the bright sun, heat reflected from the sand, and high winds.[6] The juniper, while perfectly at home here, apparently is so only through coincidence, for its original habitat is seemingly dry rocky hills. But the other

FIG. 7.—Typical upper inner slope of a dune beach; the grass is beach grass, but in the center is a typical plant of dwarf creeping juniper.

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[6] This principle, which from its discoverers we may call the KIHLMAN-GOEBEL principle, seems to me deserving of much more recognition than our students are inclined to give it. At least it calls for careful experimental investigation.

two, the waxberry and the Hudsonia, are characteristic of just this situation, in and to which they have apparently been adaptively developed. Towards the inner dune beaches another low shrub comes in on the slopes, though dwarfed and not abundant, the common blueberry, *Vaccinium pennsylvanicum;* it is evidently not here at home, but its somewhat xerophytic habit permits it to exist. As these various plants grow older and extend their patches, they run together more or less, sometimes two, sometimes three, and even all four. Later others are added to them, initiating the juniper mats and the woods carpet, later to be considered.

The contrast between the vegetation of the outer and the sheltered slopes of the dune beaches comes out with striking clearness a few hundred yards north of Eel Brook, where it happens the entire plain is very narrow, and slopes in both directions from a central higher crest. Outside of this can be seen only the beach grass and its accompanying forms as listed above, while inside the various xerophytic shrubs show to great perfection.

THE SWALES.

Between the open grass plain and the woods occurs a transition zone marked not only by an intermediate vegetation but also by distinctive physical features as well. First of all it is characterized by the presence of several great turf-carpeted and tree-bordered swales, morphologically hollows between the dune beaches which here spread much farther apart than usual. They are well shown in *figs. 8, 10, 11.* They are best developed in the widest part of the plain, hardly occurring towards its southern or northern ends, and outside of them runs a line of higher dune beaches, which indeed can be traced through most or all the length of the plain (*fig. 2*). The swales are narrow southward, but broaden northward, deepening as they go, until in some cases they dip beneath the water-table (thus exhibiting pools), after which they rapidly narrow and rise to disappear northward. Again, the trees of this zone, occurring always along the slopes of the dune beaches, do not exhibit a transition of size and age to those of the sandy woods, but are always so much smaller and younger as to be sharply marked off from them, the case shown in *fig. 10* being very exceptional, and that of *fig. 8* more typical. Again, the transition from the broad swales to the beaches of the sandy woods is most abrupt, for the latter are regular, narrow, close together with scarcely any hollows between, and also exhibit a curious barrenness on their summits in marked contrast to the better-clothed summits farther out (compare *figs. 8* and *13*). Unfortunately the full importance of these features did not strike me in time for a study of them on the ground, but such data as I possess in notes and maps lead me to believe that the swales are much newer in origin than the beaches immediately inside them, and that they mark the transition from an older series of beaches which formed part of the original Grande Plaine extending far to the north of the present island, and a newer series formed by the rolling of the plain down the coast, as described earlier in this paper. All the facts I possess both as to geography and vegetation are consistent with this view.[7]

FIG. 8.—Typical transition zone, looking north; showing a swale on the right, with its sharp line of transition to the woods; the trees are all white spruce.

Aside from the question of age, the swale zone differs physically from the grass plain by its greater shelter from the west winds, its lower level and greater nearness to the water-table, a probable increase of mineral nutrients derived from decaying driftwood and diffusion from the upland, and some slight accumulation of humus.

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[7] And it is sustained by the tradition of the residents who say that the plain has been built out from the edge of the woods almost within the memory of men still living. I have discussed the subject more fully in Bull. Nat. Hist. Soc. N. B. No. 24:456. 1906.

The vegetation consists broadly of a higher development of the vegetation of the inner grass plain—the scanty turf of the hollows becoming the broad expanse of meadow turf of the swales, and the juniper mats extending greatly with the addition of many young white spruces. So distinct are the turf of the swales and the juniper mats, with their trees, from one another, that there result glades and vistas of park-like and charming aspect, as shown especially well in *fig. 8*.

First in importance are the juniper mats, for they inaugurate the woods. These mats, composed either of large radiating patches of this plant, or else variously united and combined with patches of waxberry, Hudsonia, and blueberry, extend greatly in diameter, covering the crests as well as the slopes of the dune beaches, and thus form a woody net in the shelter of which several other forms, mostly markedly dwarfed, gain foothold. A typical example is shown in *fig. 9*. Some of the plants of the grass plain persist, especially the beach grass, pearly everlasting, and yarrow. The new forms which appear are, first of all, the common crowberry, ***Empetrum nigrum***, and the rock cranberry, *Vaccinium Vitis-Idaea* ***minor***, followed closely by the three-toothed cinquefoil, *Potentilla* ***tridentata***, all of them plants characteristic of dry upland rocky situations. Less frequent are the little gentian, *Gentiana Amarella acuta*, and the large cranberry, *Vaccinium macrocarpon*, plants belonging to moist places. And when the mats are especially well developed there come in, as shown in *fig. 9*, the reindeer lichen, *Cladonia rangifera*, and a brown moss which I take to be the *Aulacomnium palustre* (so much more highly developed in the woods), another curious mixture of xerophytic and hydrophytic forms. We have therefore upon these juniper mats a very heterogeneous assemblage of forms drawn from diverse natural habitats all the way from rocky hills to bogs. They do not exist here, therefore, in virtue of adaptation to this position, but plainly represent those forms of the flora of this region whose adaptations happen to fit these conditions, or whose range of physiological toleration happens to be great enough to permit endurance of the conditions here. Of these matters we shall know more in the future, but their mention helps to emphasize how large an element of accident or incident there is in adaptation, and how likely it is that adaptation will ultimately prove to be a matter of the loose and large rather than of the exact and minute.

Finally, it is in this same situation, upon the upper slopes of the dune beaches, and usually, but not always, on the juniper mats, that the characteristic trees of the zone, the white spruce, *Picea alba*, develop. Standing in open formation, they do not interfere with one another's growth, and in consequence become, except for wind effects, symmetrical in outline and clothed to the ground. They occupy that situation no doubt for the same reason that the shrubs do, as a compromise between the greater wetness of the hollows and the greater dryness of the beach summits. This habit of growing thus upon the slopes, and not on summits or hollows, has a most important effect upon the physiognomy of the vegetation in this zone; for to it is due the openness of the swales, with their regular borders of trees, and as well the openness of the beach summits in the sandy woods later to be noticed. Toward the sea the spruces are small and dense, and often show, as in *fig. 11*,

FIG. 9.—Typical large juniper mat on a slope and crest of a dune beach, with a number of associated plants noted in the text; looking south.

pronounced wind effects. In places many seedling trees may be found, though the distribution of these is curiously irregular. In one place only did I find any other tree, and that was a single specimen of the prince's pine, *Pinus Banksiana*.

If it be asked why the white spruce is the first tree to develop on these plains instead of some other of those growing on the upland near by, I can only say that an answer must wait until we know something about the physiology of the white spruce and of other trees of the vicinity.

We turn next to the swales, those long open hollows carpeted by a close turf, and bordered by spruces. The general appearance of the turf is well shown on the right in *fig. 8*, and extremely well in *fig. 10*, which shows perhaps the best-developed of all the swales. The turf is a good deal modified in vegetation by the grazing of cattle and horses, yet its general characters show plainly enough. Originating in the outer hollows with the strawberry, as already noted, the real turf begins with the red fescue grass, *Festuca rubra* (*F. ovina rubra*), which soon drives out the strawberry. To this, as it becomes compact in the inner hollows, other grasses are rapidly added, especially the June grass, *Poa pratensis*, and then the brown top, *Agrostis alba*. After these comes a rush, *Juncus Vaseyi*, and the little sedge, *Carex Oederi*. Very likely, also, there are other

FIG. 10.—Highly developed swale, looking south: on the left is the edge of the sandy woods with old trees, and on the right a line of much younger trees, here much larger than usual.

grasses which, owing to my imperfect knowledge of those groups, I overlooked. On and among these plants occur others, among which I have collected the following: the eyebright, *Euphrasia americana* (*E. officinalis*); the bugle weed, *Lycopus uniflorus* (*L. virginianus*); a tiny everlasting, *Antennaria neodioica;* a pearlwort, *Sagina procumbens;* the plantain, *Plantago major;* the two common cinquefoils, *Potentilla norvegica* and *Anserina;* the fall dandelion, *Leontodon autumnale;* and the white clover, *Trifolium repens.* These forms, in common with the grasses, are all greatly dwarfed and derived from diverse habitats, and are evidently a collection of heterogeneous stragglers from the neighborhood, held together by no stronger bond than ability to eke out existence in this inhospitable position. The majority belong to somewhat moist places, and they find an ample supply of water; for the water-table even in the driest summer is within a foot of the surface, and of the sweetest water. Evidently it is not dryness which stunts the forms, but most likely, as I believe, paucity of mineral nutrients. The turf represents the first closed formation we have met with, and

FIG. 11.—An outer swale, looking north; in the center clumps of blue flag; on the slope on the left white spruce and waxberry; on the right is a low depression with a thicket of poplar (the white spruce among it being on a local elevation).

competition may therefore determine some of its minor features, but to these I gave no attention.

The turf reaches its climax in the open swales like those shown by *fig. 10.* In the woods it disappears, as will be noted under the next section; but towards the lower levels, especially towards the pools of standing water, it gives way gradually, by definite steps, to an assemblage of true swamp plants. The very first of these to appear in the lower places in the swales is always the common blue flag, *Iris versicolor,* and characteristic scattered clumps of this plant may be seen in the foreground in *fig. 11,* in the distance on the swale in *fig. 8,* and on the left margin of the swale in *fig. 10.* Next follows always the sweet gale, *Myrica Gale,* and after that low bushes of the balsam poplar, *Populus balsamifera,* a plant which forms very dense thickets and grows larger as the situation is more sheltered. Finally the pools of standing water are reached, and on their margin occur cat-tails, rushes, and mare's tail, *Hippuris vulgaris,* with some other forms which I have not attempted especially to study. The plants may be variously combined according to local circumstances, but a very typical arrangement is shown in *fig. 12.* It is plain that we are dealing here simply with an ordinary

FIG. 12.—Marshy swale, looking south; in the center a permanent pool with margin trodden by cattle; behind it are cat-tails and rushes, and back of them a thicket of poplar; on both right and left is sweet gale, and in the foreground is the blue flag.

swamp, offering nothing peculiar unless it be the small size of some of the plants, notably the poplar. But these places develop yet farther in time, and there come in after the poplar three willows: *Salix balsamifera*, *S. lucida*, and *S. candida*, forming very dense thickets, and apparently under congenial conditions. Finally comes in the alder, which appears to be mostly a form of the green alder, *Alnus mollis*, giving us the culmination of the swale thickets.

THE SANDY WOODS.

Inside the swale zone, through almost the whole length of the plain, extends a narrow zone, only some four or five dune beaches

FIG. 13.—Typical sandy woods, just inside the swales, looking north; in the center a dune beach, bearing scanty beach grass and reindeer lichen, while on the slopes are small juniper mats with white spruces.

wide, of remarkable sandy woods, whose characters are well shown by *fig. 13*. Their most striking feature is perhaps the relative bareness of the tops of the beaches, which remain far more clear of vegetation than do most of the beaches outside of them; and this bareness, in conjunction with the presence of trees on the slopes and in the hollows, gives rise to curious vistas as shown by the photograph. The bareness must have some physical basis, but I was not able to discover it. These dune beaches, further, are very narrow, low, and regular, with hardly any true hollows between, so that the turf from the swales is very scanty, almost wanting, in this zone. Further, the trees, all of them white spruces, are much older than those of the swale zone, the transition being commonly of the most marked abruptness. All of these features tend to emphasize the conclusion earlier given, that there is an abrupt physical difference between the beaches of these woods and those outside, a difference which, I feel sure, is one of age. The position of the zone would indicate that it possesses more favorable physical conditions as to water, mineral supply, and shelter than the zone outside, with which the large size of the trees is in agreement. But the bigness of the trees makes the barrenness of the beaches all the harder to explain. In their vegetation the sandy woods exhibit three divisions: the sparse, scattered beach grass and reindeer lichen (*fig. 13*) on the beach crests already mentioned; a few and small patches of turf which can hardly obtain a foothold where the hollows are so small; and the juniper mats in the slopes and hollows with their well-grown white spruces. The mats, however, are no longer entirely creeping, for the junipers send up numerous erect shoots. With them persist several of the plants from the transition zone, especially the rock cranberry, the three-toothed cinquefoil, the pearly everlasting, and a few others. But in addition new forms come in, especially and characteristically the bearberry, *Arctostaphylos Uva-ursi*, a rocky-hill plant, here creeping radiately over the sand, apparently under congenial conditions. Beneath the shelter of the trees appear some plants of the woods carpet which we may best consider under the next section. The trees themselves are of moderate size, rarely if ever over 20 feet in height.

A fact of interest about the juniper mats, applying also to a less degree to the forest mat which succeeds it in the closed woods, is its very slight hold upon existence on the sand, for where teams cross and disturb it, the entire mat dies and soon disappears. Such instability shows forcibly how hard are the conditions of life in this situation, and how narrow the margin between success and failure.

THE CLOSED WOODS.

The climax of the sand-plain vegetation is reached in the dense though dwarfed mixed woods extending between the sandy woods and the upland. A typical view of the closed woods is shown by *fig. 14*.

Physically the situation is much more protected than the zones outside of it, and, lying at a still lower level, it has a moister soil. The soil, however, is still of sand, though it contains some humus from the decaying vegetation and must derive some mineral matter by diffusion and drainage from the upland. Very likely also the sand is shallower here than farther out (*fig. 2*), and hence some influence of the minerals of the underlying soil may be felt, while in places an appreciable enriching of the soil must result from the decay of the bodies of the walrus, formerly slain here in great numbers, as manifest by their semi-fossil bones.[8] These additional sources of mineral nutrients, however, by no means furnish a supply sufficient for the proper growth of the woods, for in every feature they exhibit marked depauperation as compared with the same species on the neighboring upland.

FIG. 14.—Typical closed woods, chiefly of white spruce, but with some deciduous trees in the background; the closed forest carpet shows in the glade of the left foreground.

In relation to the preceding zone, the closed woods consist essen-

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[8] Described more fully in a note in Bull. Nat. Hist. Soc. N. B. No. 24:462. 1906.

tially of a greater development of the juniper mats, which unite to form a complete unbroken carpet, together with a greater development, both in number and size, of the white spruce trees, to which are added some deciduous trees and shrubs. And where the hollows dip lower than usual, and towards the upland in places, this forest merges to alder and cedar swamp.

We consider first the woods carpet. Morphologically it is a direct development of the juniper mats of the outer zones, though but little juniper, aside from occasional erect shoots, is left. With it persist some of its earlier associates, the rock cranberry, three-leaved cinquefoil, some grasses, the bearberry, and the reindeer lichen, varying in their respective development according to situation. To these are now added dwarf plants of the bunchberry, *Cornus canadensis*, the twin flower, *Linnaea borealis americana*, *Pyrola chlorantha*, the pipsissewa, *Chimaphila umbellata*, and an abundant brown moss, which has been identified for me by Mr. A. J. GROUT as *Aulacomnium palustre*, a typical swamp moss. Upon this carpet develop a few larger forms, especially the abundant wild sarsaparilla, *Aralia nudicaulis*, the gooseberry, *Ribes oxyacanthoides*, the dwarf raspberry, *Rubus triflorus*, with others less conspicuous.

We consider next the trees of these woods. First in importance and size, far surpassing all others in both respects, is the white spruce. It attains a height of perhaps 7.5^{m}, a diameter near the ground of perhaps 45^{cm}, and it exhibits over 100 annual rings, though perhaps some may be much older than those I counted, which were cut by the residents for wood. The next to appear is the balsam fir, *Abies balsamea*, becoming somewhat abundant and characterized by a spruce-like arrangement of its leaves all around the stems. Then follow the red maple, *Acer rubrum*, the aspen, *Populus tremuloides*, the paper birch, *Betula alba papyrifera* (in very small trees however), and the mountain ash, *Pyrus americana;* while the common undershrubs are the red dogwood, *Cornus stolonifera*, and the black alder, *Ilex verticillata*. There are probably some others, but these I believe are all that are notable.

In especially low places, such as in certain hollows, and at the contact of plain and upland, the conditions verge towards those of a swamp, and swamp plants appear—the iris, the sweet gale, some mints, species of Galium, and the dewberry; while the spruce gives way to the white cedar, *Thuja occidentalis*, and the alder becomes abundant, forming a dense jungle. But this is of less interest than the vegetation of the outer zones, and hence I gave it little study.

Thus it appears that these woods present no features, size of the plants alone excepted, markedly different from those of woods preponderatingly coniferous in the neighboring upland, and they are evidently tending towards the typical woods of this region—the mixed coniferous-deciduous forest.

We have thus another illustration of that principle so important in physiognomic ecology, that vegetation, no matter under what immediate physical conditions it may be, is always tending towards a climax type, determined primarily by climate.

CONCLUSION.

In this paper I have tried to state the facts about the vegetation of a somewhat remarkable place, adding thereto some ecological comment whose chief value is to illustrate our ignorance of that subject. As I understand it, such descriptions as this aims to be may have three values. First, they can present to all who have interest in such matters a series of pictures, as vivid and realistic as possible, of the vegetation of special places, and they are the more valuable according as they are the more clearly and attractively written and the more aptly illustrated. Second, they should help to supply information, badly needed by all of our manuals, about the natural habitats of the common or important species of plants. Third, they can form storehouses of facts about vegetation upon which the future student can draw as the advance of physiological ecology gradually makes possible an understanding of the principles underlying physiognomic ecology. Such descriptive work can be done to profit by the student whose work is perforce confined to his summer vacations, if he but bring to it time and care enough; but he should be content to describe well and to leave interpretation to the field physiologist yet to come. Speculation cannot of itself advance knowledge, and it can bring a subject into disrepute. It is only, I believe, through field physiology, the study in field laboratories of fundamental plant-dynamics, that ecological knowledge can really be advanced. And the dynamical problems, as I see them, fall under these heads, in the order of importance: (*a*) physiological life-histories of species, (*b*) physics and chemistry of the soil, (*c*) nature of plant-competition, (*d*) a better correlation of meteorological data with physiological phenomena.

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THE DEVELOPMENT AND ANATOMY OF SARRACENIA PURPUREA.[1]

CONTRIBUTIONS FROM THE BOTANICAL LABORATORY OF THE JOHNS HOPKINS UNIVERSITY. No. 5.

FORREST SHREVE.

(WITH PLATES III–V)

THE work of which the results are here given was undertaken at the suggestion of Dr. D. S. JOHNSON, and has been carried out at the Biological Laboratory of the Johns Hopkins University. I wish here to express my thanks to Dr. JOHNSON for much advice and helpful criticism in connection with this work, and to express to Professor WILLIAM K. BROOKS my appreciation of his interest and encouragement. I also wish to thank my fellow-student Mr. SAMUEL RITTENHOUSE for his kindness in gathering material for me during my absence from Baltimore.

The material worked upon was obtained mainly at Glenburnie, Maryland, near Baltimore. Most of it was fixed in the field; and of several killing reagents tried 1 per cent. chrom-acetic and Carnoy's mixture were the most satisfactory. Preparations mere made by ordinary paraffin method and stained with the Flemming triple stain or with cyanin and erythrosin.

DEVELOPMENT OF THE FLOWER.

The earliest stage observed in the development of the flower was in material gathered August 30. There are then to be seen the primordia of the three bracts, the five sepals, and the five petals, which have apparently arisen in the order named. Lying just within the edges of the petals are the staminal primordia, as yet mere papillae, and within them is a flat surface with slight elevation at the center. A somewhat later stage than the last shows progress in the development of the stamens, which now appear as ten groups of protuberances lying in the position before noted (*fig. 2*). Each

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[1] Dissertation submitted to the Board of University Studies of the Johns Hopkins University for the degree of Doctor of Philosophy.

group arises from a base which is distinct from the bases of the adjoining groups, and is made up of the primordia of five to eight stamens. There is no suggestion of a pairing of the groups nor of their falling in two whorls. Upon the central flat surface has arisen the ovary, which at its base is pentagonal in outline, and at its apex is surmounted at the angles of the pentagon by the tips of the carpellary leaves. The outgrowths of the wall of the ovary which are destined to give rise to the placentae are upon the sides of the pentagon, which shows each placenta to be made up of the edges of two carpellary leaves (*figs. 2, 14*).

MICROSPORANGIUM AND MICROSPORE.

The staminal primordia early show differentiation into parts destined to give rise to filament and anther. The latter portion bears approximately the same outline in cross section as do the mature anthers. The location of the archesporium is indicated at first only by the slightly greater size of the nuclei in the region of the four microsporangia (*fig. 4*), but soon comes to be more sharply defined by the concentric arrangement of cells in the region of the future parietal cells. The archesporium is at this earliest recognizable stage about six cells in cross section, but grows rapidly to about twelve cells in diameter (*fig. 5*). Development proceeds in the autumn to the differentiation of the endothecium, the two or three parietal layers, and the pollen mother cells. There is yet no distinction of definitive sporogenous cells and tapetum. In this condition the stamens pass the winter.

The elongated parietal cells do not contribute to the tapetum, but it is made up entirely from the isodiametric cells of the archesporium. The outer outline of the tapetal layer is continuous, and the inner is irregular only to an extent which makes it in some places two cells in thickness and in other places three. The cells of the tapetum do not wander among the definitive sporogenous cells Shortly after the differentiation of the tapetum, and before the pollen mother cells are in the synapsis stage, the tapetal nuclei divide once by mitosis, and so far as observed once only. At the time of tetrad division the tapetal nuclei are enlarged, the chromatin is granular and scattered, and the nucleoli are large. At the time of the formation of the walls of the pollen grain the cytoplasm of the tapetal cells becomes much vacuolated and the nuclei lose their chromatin; but at no time does the layer become broken. The parietal layers at the time of the tetrad division are three to five in number, the endothecium is thickened on its inner and lateral walls, and the epidermis is undifferentiated. The thickening of the endothecium walls takes places very late—simultaneously with the division of the pollen grain nucleus—the cells for some time previous to this being filled with starch.

Dehiscence is by means of two longitudinal slits, each of which opens two pollen sacs of the anther. A deep crease runs between each pair of pollen sacs upon the two sides of the anther, penetrating to the point at which the two microsporangia lie nearest each other (*fig. 13*). At this point is a group of small cells reaching from one microsporangium to the other, the walls of which are thrown into creases and folds, and fail to thicken in the further development of the anther, as do the neighboring cells.

The pollen mother cells apparently lie in the synapsis stage for several days. At their first division it is possible to count the chromosomes, the reduced number being twelve and their form short and blunt (*fig. 8*).

The tetrad division is simultaneous, there being no formation of wall after the first division. After a short period of adherence in tetrads the pollen grains round off and acquire the coats. The mature pollen grain is marked with eight meridional grooves so as to resemble a muskmelon. Beneath the grooves the intine is several times thicker than between the grooves (*fig. 11*). While the pollen grain is yet within the anther the nuclear division takes place which gives rise to tube and generative nuclei (*fig. 12*). In this condition the grains are shed, the stamens nearest the ovary opening first, and the outer ones successively.

OVULE AND MEGASPORE.

The placental outgrowths which arise from the flat sides of the ovary, at the point of juncture of the edges of the carpellary leaves, grow inward almost to the center of the ovary, and these I shall designate as the "main placental outgrowths" (*fig. 14*). Each main placental outgrowth sends out two lateral outgrowths so as to resemble in cross section a letter T, in which the arms have been bent downward. Each pair of adjoining lateral outgrowths is closely appressed and directed backward toward the angles of the ovary. In the lower part of the ovary the adjacent lateral outgrowths fuse, but do not extend to the bottom, and in the upper part they do not reach the wall of the ovary as do the main placental outgrowths. Upon the edges of the lateral outgrowths and upon the surfaces lying next the main outgrowths are borne the ovules (*fig. 15*). The ovules at the base and top of the ovary lie parallel to the axis of the flower, those in the middle lie at right angles to it, the intermediate ones having intermediate positions according to their place in the ovary.

The summits of the carpellary leaves broaden and coalesce, and grow out in a direction radial to the axis of the flower, so that while their basal parts form the capsule and the stalk of the style, the tips form the umbrella of the style (*fig. 3*). The tip of each carpellary leaf organizes a very definite growing-point (*fig. 28*), and the portion between the tips nearly keeps pace in growth. Upon the ventral surface of each tip, just before it completes its growth, is formed the protuberance which bears the stigmatic surface.

The appearance of the primordia of the ovules upon the placentae takes place from the point opposite the angle of the ovary wall, where the adajcent lateral outgrowths meet, successively toward the angle formed by the lateral outgrowth and the main outgrowth (*fig. 19*). In vertical direction the development proceeds from the middle of the placenta toward top and bottom. The ovules first appear as protuberances initiated by the periclinal division of subepidermal cells and the accompanying anticlinal division of the epidermal cells, as is commonly the case. When the ovule first protrudes from the placenta there is no suggestion of a sporogenous cell. At this stage of development the winter rest intervenes. The first suggestion of a sporogenous cell comes with the enlargement of a single subepidermal cell, which is the megaspore mother cell (*fig. 16*). In three cases out of many hundreds examined there were two mother cells lying side by side. There is no tapetal cell. The bending by which the ovule becomes anatropous begins at once, and is quite marked by the time of the appearance of the mother cell. Both transverse and longitudinal sections (*figs. 16* and *17*) show a double layer of cells at the sides of the mother cell, and median longitudinal sections show approximately five rows of cells in the ovule, exclusive of the epidermis.

The integument is single, its development beginning by periclinal divisions of subepidermal cells upon the convex side of the bending ovule, and continuing as a ring which grows rapidly on the side where it began first and slowly on the opposite side, which lies next the raphe. The rapid growth of the ovule is accomplished largely by the chalazal end. By the time of the first division of the mother cell the bending of the ovule is completed, the integument has grown so as nearly to close the micropyle, and the mother cell has increased in size and encroached upon the nucellar tissue so as to lie next the epidermal cells over the entire distal end (*fig. 20*).

The difference in the time of appearance of the ovules upon the different parts of the placenta causes a difference in the degree to which the integuments develop (*fig. 19*), and also a difference in the maturation of the mother cell, and the germination of the megaspore in ovules in the different parts of the placenta, a difference which long remains evident.

At the first division of the mother cell it was not found possible to count the number of chromosomes. The division is followed by the formation of a wall (*fig. 20*), and in about half the cases observed both the daughter cells again divide to form the normal linear tetrad of megaspores (*fig. 23*). In the remaining cases the micropylar daughter cell fails to divide, resulting in a series of three megaspores (*fig. 21*); and much less frequently the micropylar daughter cell divides by a wall parallel or nearly parallel to the long axis of the nucellus (*fig. 22*). In any case it is the chalazal megaspore which functions, the micropylar ones being appressed to the layer of nucellus and absorbed. The maturation of the megaspore is coincident with the tetrad division of the microspore mother cells.

EMBRYO SAC.

Such has been the elongation of the ovule by the time the megaspore matures that the nucellus is lengthened five or six times its diameter, being made up of slightly elongated cells five or six rows thick in median section. The integument, about five cells thick, has now grown well beyond the tip of the nucellus, and its lips have become somewhat appressed to form the long micropyle. The cells in the innermost layer in the integument show active division in the direction of the greatest length of the nucellus, and by their dense protoplasm and large nuclei stand out prominently as a definite layer which I shall designate as the "columnar tissue."

After the disappearance of the megaspore sister cells the definitive megaspore continues its absorptive activity to the destruction of the single layer of nucellus at its micropylar end, so that the distal half of it comes to lie directly against the columnar tissue of the integument. The chalazal end is pointed, occupies at this time a median position in the nucellus, and is apparently active in the degeneration of the nucellar tissue, in accommodation to its own growth. About this time the definitive megaspore undergoes division. The daughter nuclei take places at opposite ends of the embryo sac (*fig. 24*), and quickly undergo the second (*fig. 25*) and third divisions in the normal manner.

The mature embryo sac is typical in every respect. It is elongated to four or five times its width, the sides lie next the columnar tissue and the base continues to be pointed and median. The synergidae lie side by side and the egg protrudes a little way below them, nearer the center of the sac. The cytoplasm of the synergidae is dense and stains heavily with the Flemming triple; that of the egg is greatly vacuolated. The antipodals lie well together in the conical base of the sac (*fig. 26*). The polar nuclei meet midway between the ends of the sac, and after their fusion the endosperm nucleus continues to occupy this position (*fig. 26*). After the fusion of the polar nuclei the endosperm becomes very active in the disorganization of the remaining basal portion of the nucellus. In this activity the antipodals do not take part. The base of the sac remains pointed, but from being median now comes to lie against the columnar tissue at one side of the nucellus by means of the absorption of the nucellar tissue which lay between its previous position and the columnar tissue. The further enlargement of the sac is accompanied by a pushing downward of the base between the nucellus and columnar tissue, and in some preparations the antipodals would seem to have been pushed to one side (*fig. 27*). The columnar layer now shows its maximum development, being made up of deep, much-flattened cells with darkly staining cytoplasm. The function of these cells is no doubt that of secreting and passing over to the sac sugars or other elaborated foodstuffs.

POLLINATION AND POLLEN TUBES.

Pollination takes place, near Baltimore, during the first week in May. In the mature style of Sarracenia at the time of pollination the umbrella is a pale green color. Its internal structure is leaf-like without a definite palisade, but with abundant intercellular spaces and stomata numerous upon the upper surface and few upon the lower. Long unbranched unicellular hairs cover the lower surface so thickly as to form a tomentum in which considerable pollen is caught at the time of shedding. There are also upon both sides of the umbrella multicellular glands of spheroidal shape projecting slightly above the level of the epidermis. Running from the five stigmatic surfaces toward the center of the umbrella are heavy veins which comprise both vascular and conducting tissue.

The union of the carpels in the formation of the stalk of the style is such as to leave at its center a pentagonal cavity which in the mature flower connects the interior of the capsule with the external air. An examination of the veins of the umbrella two weeks before pollination will show the conducting tissue as a cylindrical strand about ten cells in diameter. The cells are much elongated, with pointed ends, or many cells of this description have divided transversely to two or four cells. The cytoplasm is dense, the nuclei are large, elongated, often three times as wide as long, binucleolate, and poor in chromatin. At the time of the passage of the pollen tubes the conducting strand has become enlarged to more than twice its previous diameter at the expense of the surrounding tissue, and the cells have become still more elongated. The cytoplasm is much vacuolated, the nuclei are attenuate at the ends and devoid of nucleoli (*figs. 32, 33*), and there are large intercellular spaces. The vascular tissue of the veins lies beneath the conducting tissue and is continuous with the vascular tissue of the stylar stalk.

Two weeks before pollination transverse sections of the stalk of the style show five strands of heavy-walled cells running from the angles of the central cavity half way to the periphery (*fig. 34*). The tissue which these cells represent in cross section is four to six cells thick and runs the entire length of the stalk, being in the median line of the carpels. About the time of pollination these sheets of cells are found to split into two layers, which separate in such a manner as to form canals which are connected with the central cavity (*fig. 35*). The surface layer of cells on the interior of the canal becomes detached and undergoes partial degeneration. The five conducting canals thus formed are continuous with the conducting tissue of the veins of the umbrella above, and open below midway between the main placental outgrowths.

The stigmatic surface is richly provided with long, curved, heavy-walled outgrowths of epidermal cells (*fig. 31*), which serve to catch pollen and hold it. Pollen was found to be present in abundance on all stigmas examined. There is no definite sprouting-pore in the grains, but the tubes grow more commonly from the meridional grooves. The pollen tubes grow between the cells of the stigmatic surface and their entire passage is between the cells of the conducting tissue and never through them. They follow the well-defined course of the conducting tissue along the vein of the umbrella and down the stalk of the style (*fig. 30*).

The generative nucleus was not seen in any case to have divided before the sprouting of the pollen tube, and the earliest position in which it was seen to have divided was in a tube which had nearly reached the center of the umbrella. The tube nucleus is spherical and precedes the generative nuclei. The latter are alike in form—elongated and curved or often bent twice in serpentine manner. The distance of the nuclei from the end of the tube is four to six times the diameter of the tube. The cytoplasm is dense in the entire end and around the nuclei (*fig. 36*).

When the pollen tubes enter the cavity of the ovary from the five conducting tubes of the stalk, they are directly above the line of juncture of the two adjacent lateral placental outgrowths. The course of the pollen tubes is at first a downward one between these outgrowths, and later an outward one radial to the axis of the ovary (*fig. 30*). In this manner the edges of the placentae are reached after a course in the ovary which, for the tubes growing to the lowermost ovules, is as much as 6 to 8^{mm}, and lies entirely outside the tissue of the plant in an ovary the cavity of which has direct communication with the external air. The epidermal cells of the placental surfaces between which the pollen tubes pass are densely filled with cytoplasm; beneath them lie three layers of flattened cells of similar contents. Thin transverse walls are formed in the tubes near the stigmatic surface (*fig. 37*), and far down in the ovary, near the ovules, plugs are not infrequent in the tubes, being three to six times the diameter of the tube in length.

The distance traversed by the pollen tubes which reach the lowermost ovules in flowers of average size, is about 4^{cm}. Provision for the nutrition of the tube during its growth and passage is perhaps made in part by the photosynthetic activity of the umbrella. Previous to pollination the epidermal, subepidermal, and some deeper cells of the umbrella are filled with densely-staining, finely granular contents. In fresh material of the same age the contents of these cells fail to react to tests for sugar made with Fehling's solution, *a*-naphthol and thymol, as well as to tests for starch. Similar contents fill the epidermal cells of the stalk of the style. The course of the tubes as far as their entrance to the ovary is doubtless through a strong solution of sugars. Below the point of entrance to the ovary the passage between the placental walls is probably through a film of sugary solution held there by capillarity and supplied with materials from the epidermal cells of the placental walls, which after pollination are highly vacuolated, in marked contrast to their condition before pollination.

FERTILIZATION.

The fusion of the male and female nuclei in fertilization is preceded by the division of the endosperm nucleus in nearly all the embryo sacs. Fertilization takes place, then, in all ovules at nearly the same time irrespective of a difference in the development of the endosperm due to the position of the ovule upon the placenta. As to the length of time intervening between pollination and fertilization I am unable to give any exact data. A visit on May 24 to plants growing in the open found the anthers nearest the ovary to have shed their pollen. Material collected at the same locality two days later was found to show fertilization. The time of pollination of the particular flowers gathered and fixed may have been as much as five days before gathering, but was probably not earlier.

The thin-walled slender pollen tubes may be found in abundance about the mouths of the micropyles, often forming considerable masses. The cells which line the micropyle are heavy-walled and of such darkly-staining contents that it is difficult to observe the pollen tube within the micropyle, and indeed the entrance of the tip of the tube, with the nuclei, was not observed. The synergidae become appressed to the wall of the sac. The end of the tube upon entrance to the sac becomes expanded and pushes downward to one side of the egg. The generative nuclei have lost the elongated shape they were seen to have while passing down the style and have become spherical. Fusion of the first generative nucleus shows no special peculiarities (*fig. 38*).

ENDOSPERM.

The fusion of the polar nuclei is quickly followed by division. The first wall in the endosperm is transverse to the length of the sac and divides it into equal halves (*fig. 39*). The daughter nuclei divide in like manner (*fig. 40*), as do also the grandaughter nuclei, giving rise to an endosperm of eight cells in linear series, in which the walls are all transverse, although not uncommonly somewhat oblique (*fig. 41*). Subsequent divisions are less regular, and by the time the fertilized egg has divided the endosperm contains approximately 150 cells, its base having used up the nucellus either completely or all but a half dozen cells (*fig. 42*). At this time the endosperm cells are highly vacuolated and the laying down of food has not begun.

The relative rate of development of the endosperm in ovules upon different parts of the same placenta is the same as was noted with regard to the integuments. An ovule at the point of juncture of the adjacent lateral placental outgrowths may have an eight-celled endosperm at the same time that the endosperm nucleus has not yet divided in an ovule upon the edge of the placenta nearest the main placental outgrowth.

EMBRYO.

The first division of the fertilized egg is in a direction parallel with the length of the sac. The two-celled embryo (*fig. 43*), at first oval, becomes gradually elongated, divisions following in the same plane as the first, but not in a manner in which it has been possible to discover any regularity. After the embryo has attained a length of five to seven cells, there is a lateral division of the terminal cell (*fig. 44*), the beginning of the embryo proper. The suspensor is usually curved, though not always to so great an extent as shown in the figure. I have been unable by lack of material to observe stages in the development of the embryo immediately following the transverse division of the terminal cell.

In material of June 25 the embryo proper is found to have reached a size of approximately 250 cells, with ellipsoidal form (*fig. 45*). Dermatogen and periblem are well-defined, but no procambial cells have as yet appeared. The endosperm has by this time increased greatly in diameter, encroaching upon the tissue of the integuments. The endosperm cells have become well-stored with aleurone except in the central portion of the micropylar end—the region destined to be occupied by the full-sized embryo of the mature seed. In embryos as large as that shown in *fig. 45* the suspensor is surrounded by endosperm cells in which aleurone has been laid down; the embryo proper is surrounded by cells of highly vacuolated contents.

SEED AND SEEDLING.

Material gathered during the last week of July exhibits seeds which are practically mature. The embryo has grown to an elongated ellipsoidal form, the cotyledons being about one-third the length of the whole (*fig. 46*). Elongated procambium cells stretch from the basal end of the embryo to the region of the stem growing-point. Stomata are not formed in the embryo until the time of germination. A few endosperm cells at the sides and cotyledonary end of the embryo are free of aleurone, as they remain in the mature seed.

The surface layer of cells of the integument forms the seed coat. Its cells become irregular on their external surface and the walls are greatly thickened, with conspicuous pores in the lateral and basal walls, but none in the walls forming the surface of the seed (*fig. 47*). The inner cells of the integument are all disorganized by the growth of the endosperm and reduced to a layer of the remaining walls of flattened cells. The raphe of the ovule develops into a wing upon one side of the seed, as seen in *fig. 47*. In the mature seed there is a coating of wax upon the surface which renders them unwettable, a condition in which they remain for several weeks after they have been placed in wet moss.

Provision for the shedding of the seed is made by a deep furrow surrounding the raphe just at its junction with the placenta (*fig. 48*). The dehiscence of the capsule is loculicidal and is provided for by a deep suture upon the external surface of the capsule wall at a point where the wall is traversed by a heavy vascular bundle. Dehiscence takes place late in September or early in October, the seeds are scattered gradually during many weeks by chance shaking of the scape by wind or animals. The old flower, with umbrella and sepals still persisting, is often found side by side with the bloom of the following year.

On germination the seed is elevated above the soil or moss by growth of the hypocotyl, which is sharply bent and is the first part of the seedling to protrude. The tips of the cotyledons remain for some time in the seed, functioning as haustoria for the removal of the stored food of the endosperm. The tips of the cotyledons are active in the removal of the endosperm both at their ends and along their sides (*fig. 49*). The cotyledons expand to liguliform leaves about 1^{cm} long (*fig. 50*), and persist until about the time of the formation of the third epicotyledonary leaf. The cotyledons develop stomata during the process of germination and the epidermal and subepidermal layers of isodiametric cells bear chlorophyll.

DEVELOPMENT OF LEAVES.

The stem growing-point of Sarracenia is massive and acutely dome-shaped in the seedling (*fig. 51*). There is a definite layer of dermatogen and a common group of initials for periblem and plerome. The first epicotyledonary leaf arises opposite the interval between the cotyledons. It is finger-shaped with a somewhat broadened base. On reaching a length about twice its diameter there begins a rapid lateral outgrowth of the tissue of an **O**-shaped area on the side of the leaf rudiment which faces the growing-point, giving rise to a pit which is destined to become the cavity of the pitchered leaf (*fig. 52*). The basal part of the 0-shaped outgrowth now begins to grow upward, in which it is accompanied at the same rate by the upper portion of the 0, which at the same time carries forward the apical growth of the leaf (*fig. 53*). The cavity of the pitcher thus grows in depth by the upward growth of the tissue by which it is surrounded. The bottom of the cavity is subsequently elevated to some extent by the further growth of the tissue beneath it, but there is no sinking of the bottom of the cavity, considered as a possibility by ZIPPERER.[2] The entire early development of the leaf resembles closely that which has been described for *Darlingtonia californica* by GOEBEL.[3]

The first epicotyledonary leaf reaches its maximum size at a length of about 2.5^{cm}, and is slender in form, the cavity reaching well down toward its base, and the wing being but slightly developed. At the summit it is hooded in such a manner as to resemble the mature leaf of *S. variolaris*. The walls of the pitchers of the seedling are six to eight cells in thickness, with open mesophyll, chlorophyll in all the cells, and stomata over the entire external epidermis. There are two principal strands of vascular tissue, one in the base of the wing and one on the opposite side of the pitcher, with smaller anastomosing strands between these. In the throat of the pitcher all the epidermal cells are produced into long projecting points; lower in the pitcher occasional epidermal cells, smaller than the others, give rise to long heavy-walled hairs, while in the bottom of the pitcher the epidermal and first layer of subepidermal cells are small and heavy-walled.

While each leaf of the young plant is passing through its period of most active growth, the internode between it and the next lower leaf is also elongating rapidly. A young leaf appears for this reason to arise from the petiole of the leaf below it (*fig. 51*). The relative elongation of the internodes is far greater in the seedling than in the adult plant.

The growth of a single plant from seedling to adult was not fol-

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[2] Beitrag zur Kenntniss der Sarraceniaceen. Inaug. Diss. Erlangen. 1885.

[3] Pflanzenbiologische Schilderungen II. **5**:73–92. *pls. 19–22*. 1893.

lowed, but evidence points to the time requisite for the seedling to reach blooming age as being five or six years. Seeds of the crop of 1901, which in October of that year were placed in sphagnum in a loosely covered glass vessel, germinated in July 1902, and now, after 33 months, have no pitchers measuring over 2^{mm} in diameter. The extremely artificial conditions under which these seedlings were kept would make it inadvisable, however, to draw from them any general conclusions as to the rate of growth in the seedlings under natural conditions. The great number of intermediate stages in growth between the seedling and adult which may be observed in a single locality at any one season would also argue for the slowness of the plant in reaching adult size.

The stem growing-point of the adult plant is more broadly dome-shaped than that of the seedling, but is identical with it in the mode of origin of the dermatogen, periblem, and plerome. The earliest primordium of the leaf is likewise more massive than in the seedling, but essentially similar. Its form is conical, with a broadly semicircular base embracing the growing-point. Near the summit, upon the side toward the growing point, is developed the narrow pit which is destined to form the cavity of the pitcher, its origin being due wholly to a difference in the rate of growth of the tissue at the bottom of the pit and that forming its sides (*fig. 54*). BAILLON[4] in a brief note on the development of a Sarracenia (species not mentioned) has described this early stage and called attention to its similarity to an early stage in the development of peltate leaves, averring that "La membrane qui tapisse intérieurement l'urne n'est autre chose que l'épiderme supérieur de la feuille." This may be an entirely superficial analogy, or it may be a hint as to the ultimate origin of such a markedly modified leaf. GOEBEL (*l. c.*) has figured the early leaf primordium of *S. Drummondii*, which is essentially like that of *S. purpurea*.

With the continued growth of the leaf rudiment the pit becomes deeper, and its mouth becomes vertically elongated, although remaining very narrow. At stages somewhat earlier than that shown in *fig. 55*, the sides of the mouth of the pit have come together, closing it completely. *Fig. 55* represents a leaf primordium in which

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[4] (Note on the development of leaf of Sarracenia) Adansonia **9**:380. 1870.

the wing is just beginning to appear. *Figs. 56–61* represent cross sections of the primordium at this age in the places indicated in *fig. 55*.

In older leaves, such as are represented in *fig. 62*, the base of the leaf primordium is stoutly crescentic in cross section. Through the groove at the inner side of the leaf base the next younger leaf appears (*figs. 55* and *62*). The groove becomes narrower and more shallow as we pass up the leaf and ends just short of the bottom of the cavity of the pitcher (*fig. 62*). Above the end of the groove there is a short portion of the young leaf which is circular in cross section, above which in turn the narrow flattened outgrowth of the wing has become more conspicuous. The wing rudiment ends rather abruptly at a point where retardation of growth in diameter indicates the line of demarcation between the pitcher and cover. The cavity of the pitcher at this stage reaches as far as the upper end of the circular portion of the base.

There have been many suggestions as to the homology of the parts of the pitchered leaf of Sarracenia. A view held by many is that the pitchered portion of the leaf is derived from the primordium of the petiole and the cover from the primordium of the lamina. GOEBEL (*l. c.*) points out that since there can be no distinction in the very young leaf of primordia of petiole and lamina there can be no line drawn as to what portions of the pitchered leaf "represent" these structures.

The anatomy of the mature leaf was first worked out by VOGL;[5] it has more recently been reviewed by GOEBEL (*l. c.*), and minor contributions have been made by SCHIMPER[6] (1882) and ZIPPERER (*l. c.*). The first leaf rudiments unfolded in the spring are aborted (*fig. 62*), consisting of the sheathing base surmounted by the minute retarded primordium of pitcher and cover. These are usually three in number, and may occur in plants which do not bloom, as well as in those which do. In the latter case the aborted leaves are those just above the one to which the flower appears to be axillary.

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[5] Die Blätter der *Sarracenia purpurea*. Sitzungsb. Wiener Akad. Wiss. Math.-Naturw. **50**:281-301. *pls. 2.* 1864.

[6] Notizen über insectfressende Pflanzen. Bot. Zeit. **40**:225–234, 241–248. *pl. 4* (*figs. 1–3*). 1882.

The axillary buds of Sarracenia are commonly very small and consist of growing-point and the primordium of a single leaf, completely covered and protected by the sheathing leaf base. An occasional axillary bud develops, the first two leaves being opposite and on the opposite sides of a line connecting the growing-point of the bud with the center of the shoot. There is thus brought about a branching of the rhizome, which by frequent repetition gives rise to large clusters of individuals.

The anatomy of the rhizome of *S. purpurea* has been described by ZIPPERER in sufficient detail, since it presents no unusual fatures. He has also given a correct account of the growing-point of the root and the development of the vascular tissue of the root: the growing-point being of the type in which the cap and three tissue layers are all derived from a common group of initials; the early order of vascular bundles being triarch.

Root hairs are few upon the roots of plants growing in a saturated substratum in the open, but are abundant in seedlings grown in highly saturated sphagnum, and in adult plants in the open which are growing in a substratum merely moist. Mycorhiza has not been observed in *S. purpurea* in the vicinity of Baltimore, although fungal threads have been found covering the root of seedlings grown under the conditions previously mentioned and penetrating the epidermis. MACDOUGAL[7] (1899) has described penetration of the epidermis by hyphae in adult plants without committing himself as to their mycorhizal nature.

SUMMARY.

1. The flowers of *Sarracenia purpurea* are axillary, perfect, hypogynous, and radially symmetrical. The stamens are seventy to eighty in number and arise in ten groups. There are four microsporangia. There is a double layer of binucleate tapetal cells, derived from the primary archesporium. There are three to five parietal layers. The tetrad division is simultaneous; the microspore nucleus divides before the dehiscence of the anthers. The reduced number of chromosomes is twelve.

2. In the ovule there is a single archesporial cell, which is the megaspore mother cell. There is no tapetal cell. The ovule is

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[7] Symbiotic saprophytism. Annals of Botany **13**:1–47. 1899.

anatropous and there is a single integument. The megaspore mother cell divides to a linear series of four megaspores, or after the first division the micropylar nucleus may fail to divide or may divide by a wall longitudinal to the ovule.

3. The chalazal megaspore is functional, and develops a typical eight-celled embryo sac. The polar nuclei fuse and the endosperm may become two to eight-celled before the complete fusion of male and female nuclei in fertilization.

4. The pollen tube grows through a definite conducting tissue in the upper expanded portion of the style, through schizogenic canals in the stalk of the style and between the placental outgrowths in the ovary. The generative nucleus divides before the tube has passed into the stalk of the ovary. Fertilization presents no peculiarities.

5. The embryo is elongated and straight, with cotyledons. The storage tissue is endosperm filled with aleurone. The seed coat is the external layer of the integument. The cotyledons function as haustoria in germination and survive as chlorophyl-bearing leaves.

6. The first epicotyledonary leaf is pitchered and arises from a finger-like primordium in which a cavity is developed by unequal growth.

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Baltimore, Md.

EXPLANATION OF PLATES III–V.

Abbreviations used: *ant*, antipodal; *arsp*, archesporium; *br*, bract; *cav*, cavity; *col t*, columnar tissue; *con c*, conducting canal; *con s*, conducting strand; *con t*, conducting tissue; *cot*, cotyledons; *cov*, cover; *cp*, carpel; *der*, dermatogen; *d s*, dehiscing slit; *e*, egg; *em*, embryo; *en n*, endosperm nucleus; *e s*, embryo sac; *esp*, endosperm; *f n*, female nucleus; *g n*, generative nucleus; *int*, integument; *int i*, integument initials; *l*, leaf; *l p o*, lateral placental outgrowth; *meg mc*, megaspore mother cell; *meg sc*, megaspore sister cell; *mic mc*, microspore mother cell; *micsp*, microsporangium; *mn*, male nucleus; *m p o*, main placental outgrowth; *nuc*, nucellus; *ov*, ovary; *par c*, parietal cells; *pet*, petals; *pn*, polar nuclei; *ppi*, initials of periblem and plerome; *pro c*, procambium cells; *sc*, seed coat; *sep*, sepal; *st*, stamen; *stg s*, stigmatic surface; *stk*, stalk of style; *sus*, suspensor; *syn*, synergid; *tap c*, tapetal cells; *tn*, tube nucleus; *um*, umbrella of the style; *w*, wing.

All figures are camera drawings fom microtome sections except *figs. 29, 30, 50, 55*, and *62*, which are from free-hand drawings.

PLATE III.

FIG. 1. Vertical section of young flower bud. ×30.

FIG. 2. Transverse section of young flower bud of same age as in *fig. 1;* dotted outline represents position of carpel tips in higher sections. ×30.

FIG. 3. Vertical section of older flower bud. ×30.

FIG. 4. Transverse section of young stamen. ×232.

FIG. 5. Transverse section of single microsporangium of older stamen. ×232.

FIG. 6. Tranverse section of portion of microsporangium and wall in microspore mother cell stage. ×400.

FIG. 7. Transverse section of portion of microsporangium and wall with microspore mother cells in synapsis. ×232.

FIG. 8. Transverse section of mircosporangium and portion of wall; pollen mother cells in mitosis. ×400.

FIG. 9. Pollen mother cells in metaphase of first mitosis. ×400.

FIG. 10. Tetrads of microspores. ×400.

FIG. 11. Pollen grain. ×400.

FIG. 12. Pollen grain after division of nucleus. ×400.

FIG. 13. Transverse section of mature anther. ×20.

FIG. 14. Transverse section of young ovary. ×20.

FIG. 15. Transverse section through middle of nearly mature ovary. ×7.

FIG. 16. Longitudinal section of ovule with megaspore mother cell. ×400.

FIG. 17. Transverse section of ovule through megaspore mother cell. ×400.

FIG. 18. Longitudinal section of ovule with megaspore mother cell and integument. ×232.

FIG. 19. Transverse section of single lateral placental outgrowth, showing difference in rate of development of integument on different parts of the placenta; somewhat diagrammatic. ×40.

PLATE IV.

FIG. 20. First maturation division of megaspore mother cell. ×400.

FIG. 21. Linear series of three megaspores, arising by failure of micropylar daughter cell to divide. ×400.

FIG. 22. Tetrad of megaspores in which the micropylar daughter cell has divided longitudinally. ×400.

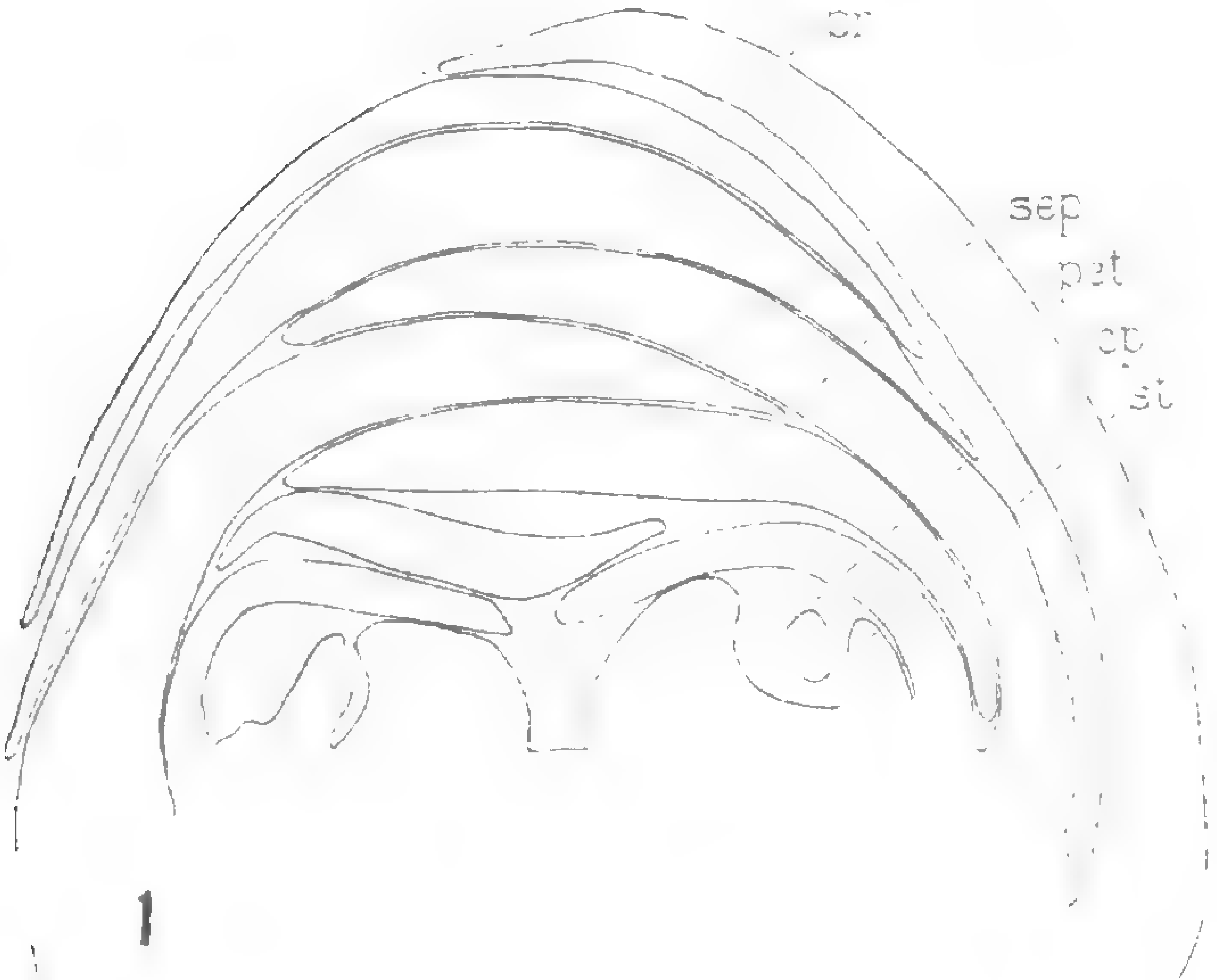
FIG. 23. Longitudinal section of ovule, with tetrad of megaspores, chalazal one enlarging and encroaching on single layer of nucellus. ×120.

FIG. 24. Longitudinal section of portion of ovule showing two-celled embryo sac, nucellus, and columnar tissue. ×232.

FIG. 25. Longitudinal section of portion of ovule showing four-celled embryo sac. ×232.

FIG. 26. Longitudinal section of portion of ovule showing fully developed embryo sac. ×400.

FIG. 27. Longitudinal section of portion of ovule showing embryo sac after fusion of polar nuclei; antipodals pushed to one side. ×232.



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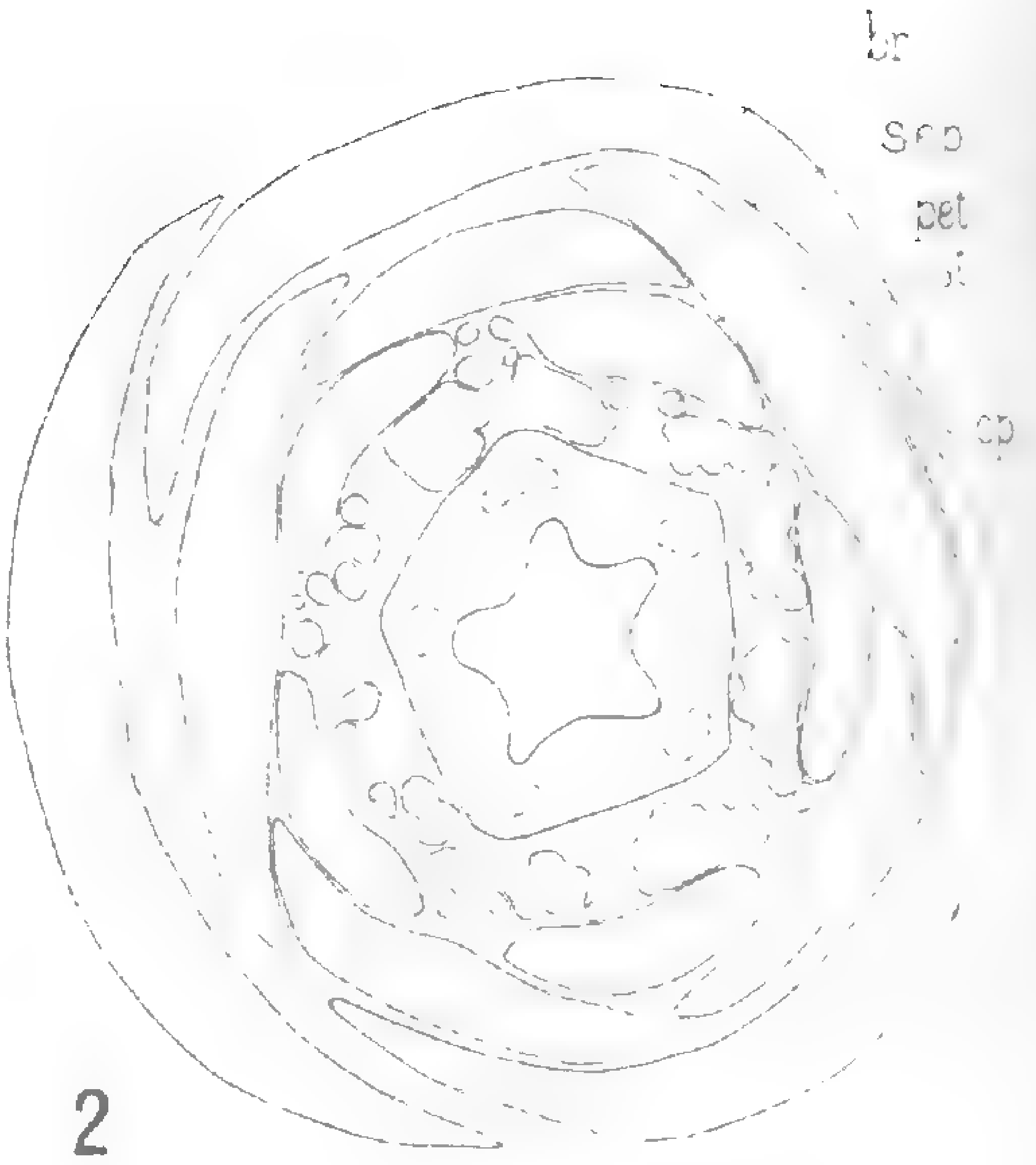

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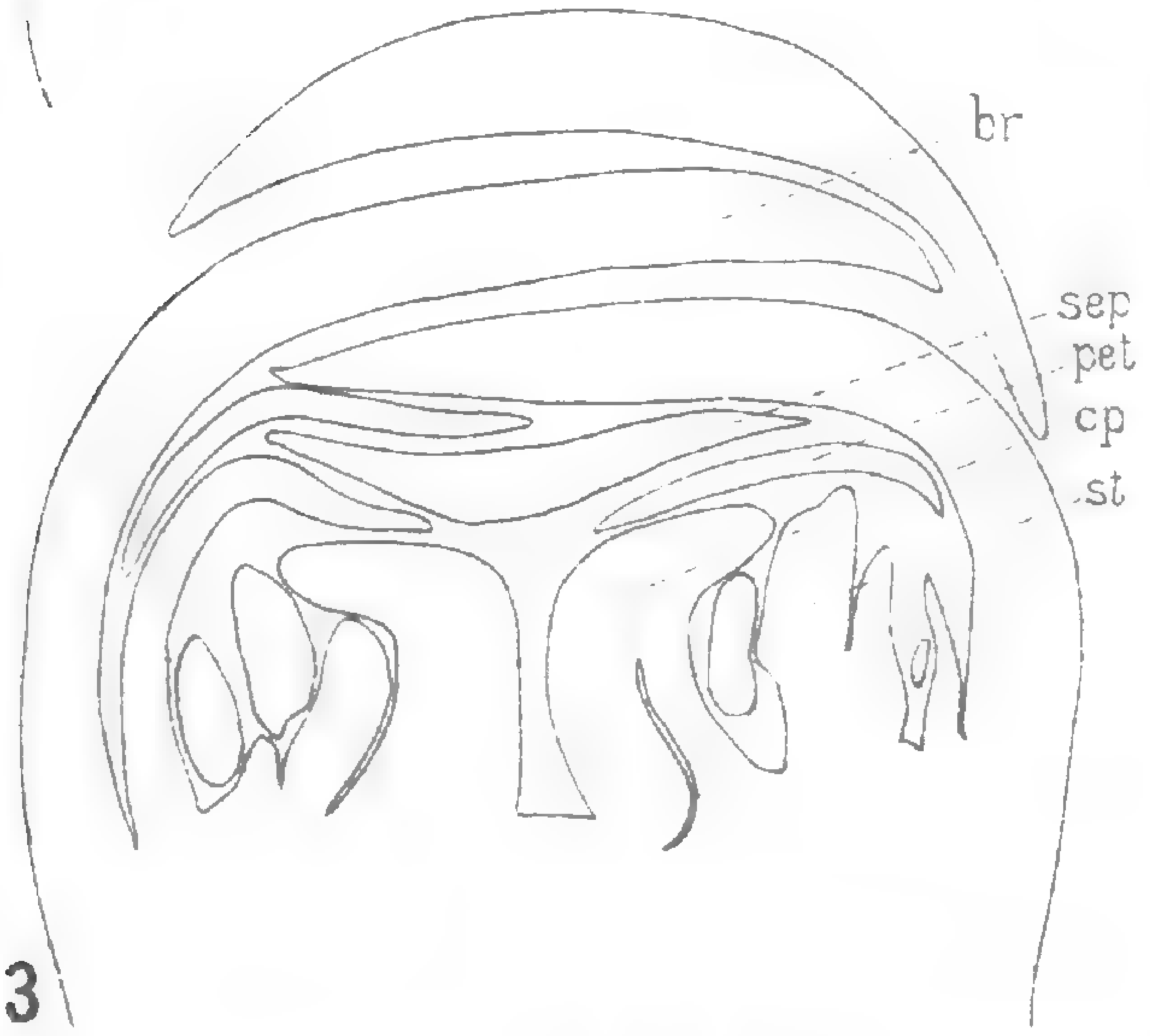

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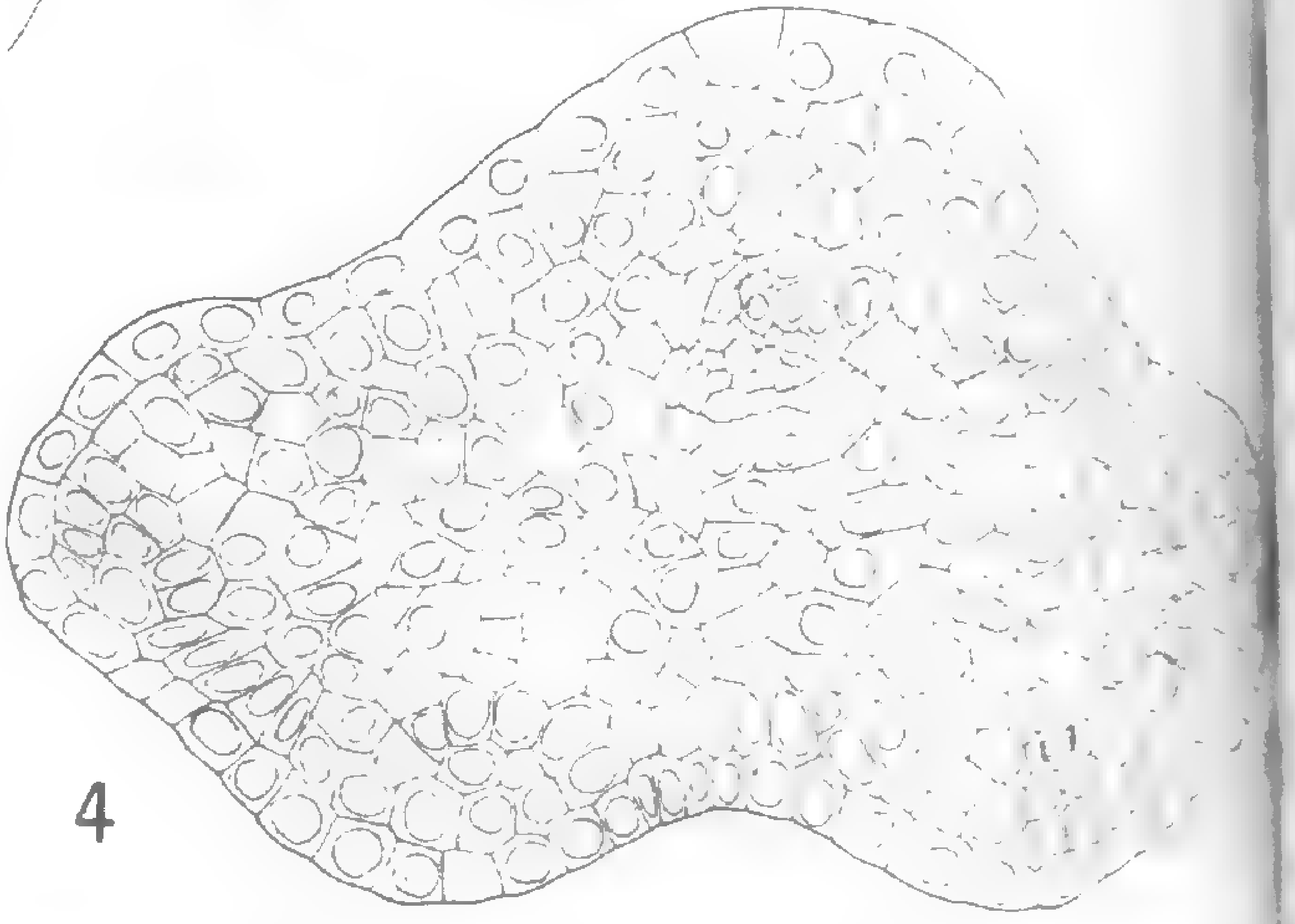

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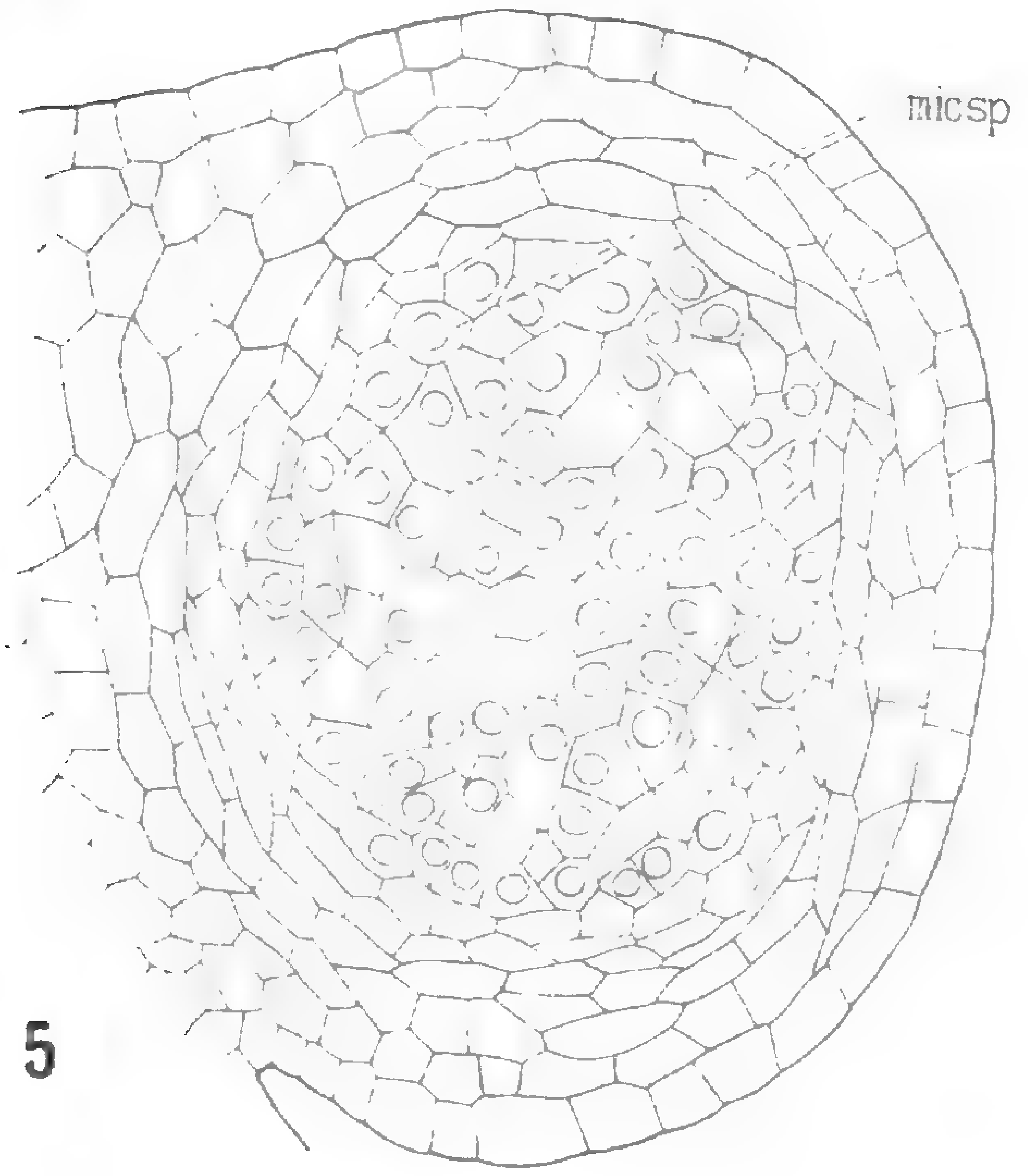

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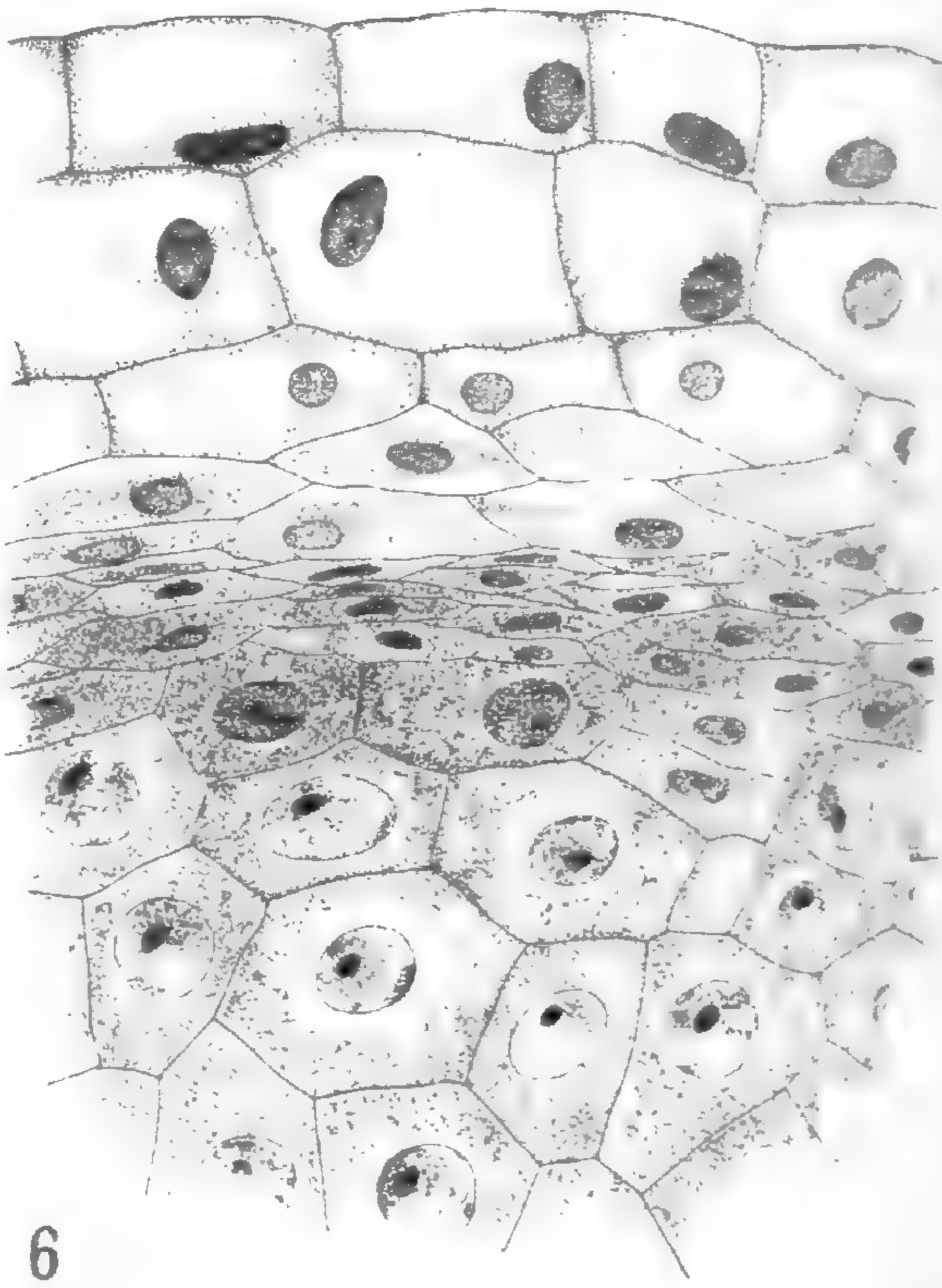

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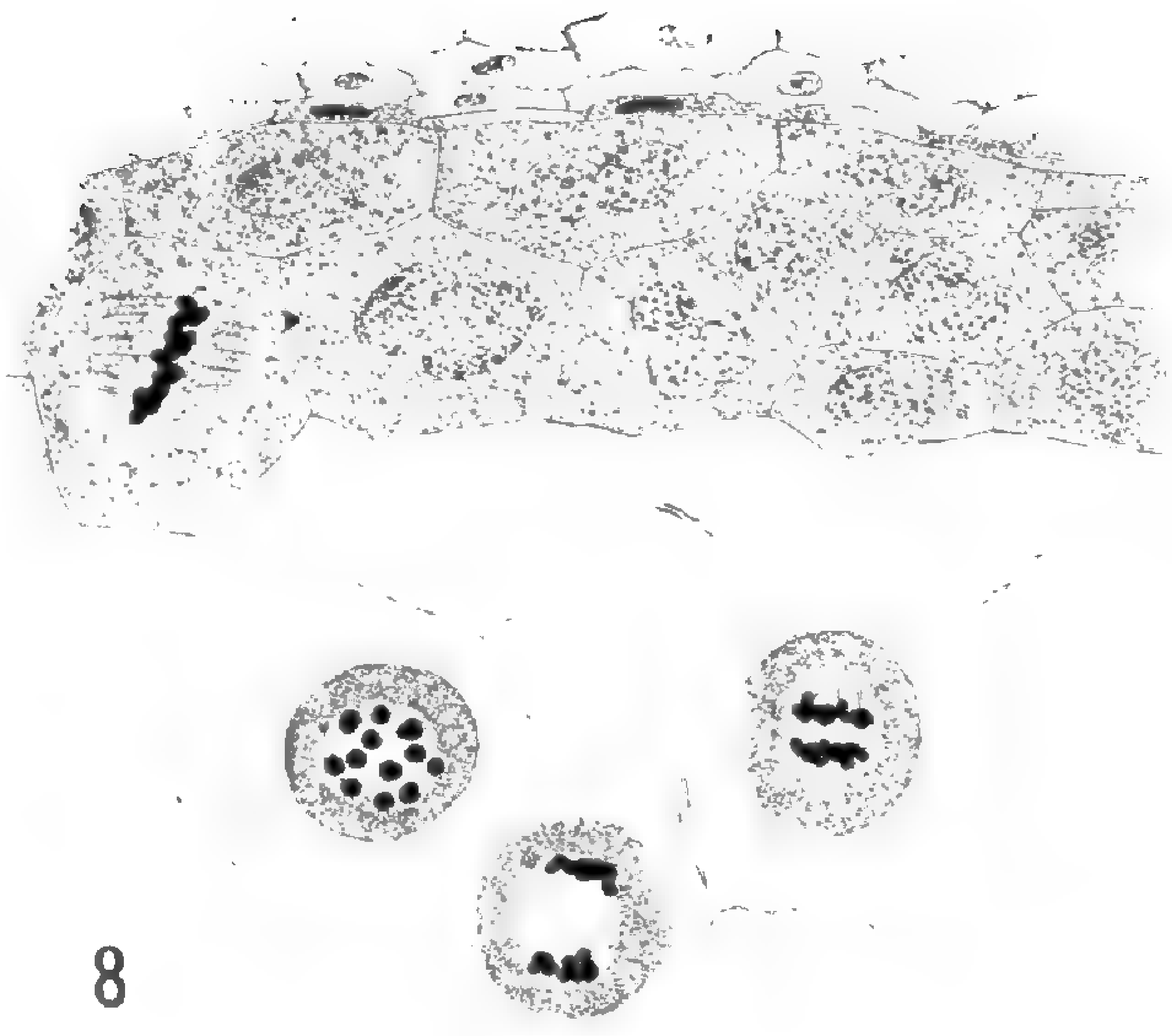

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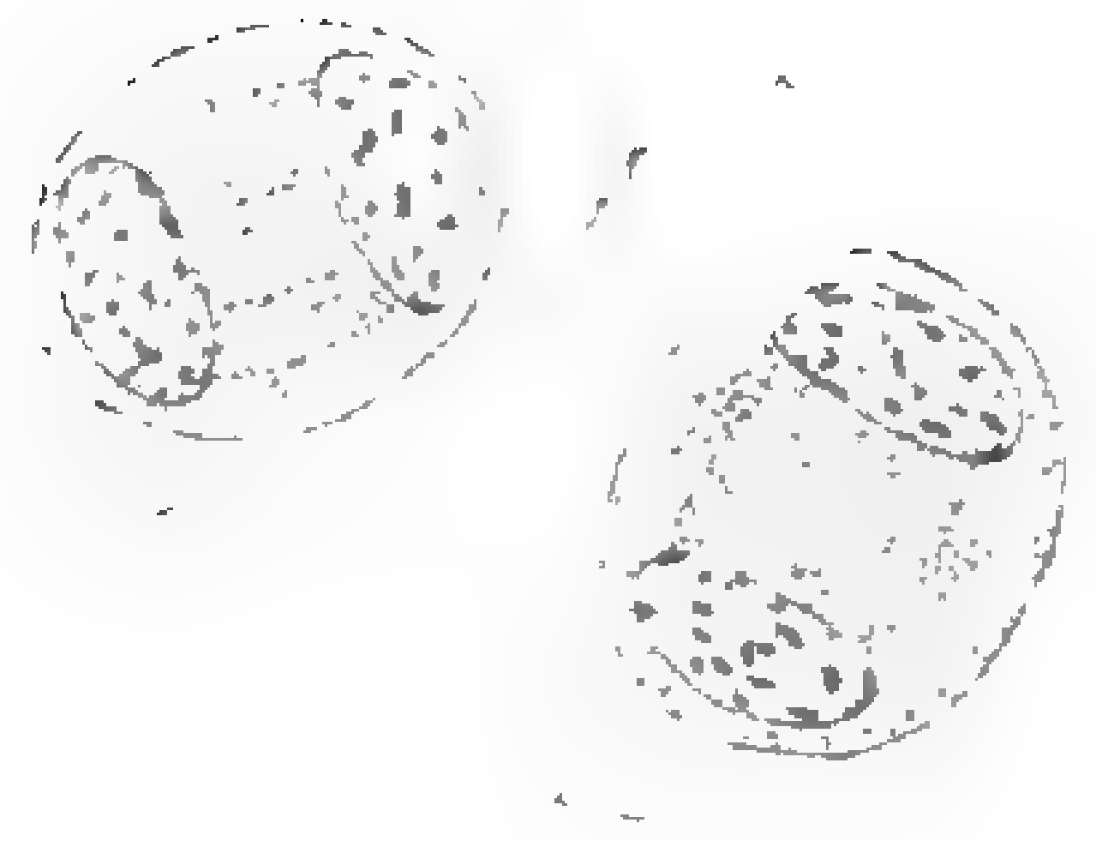

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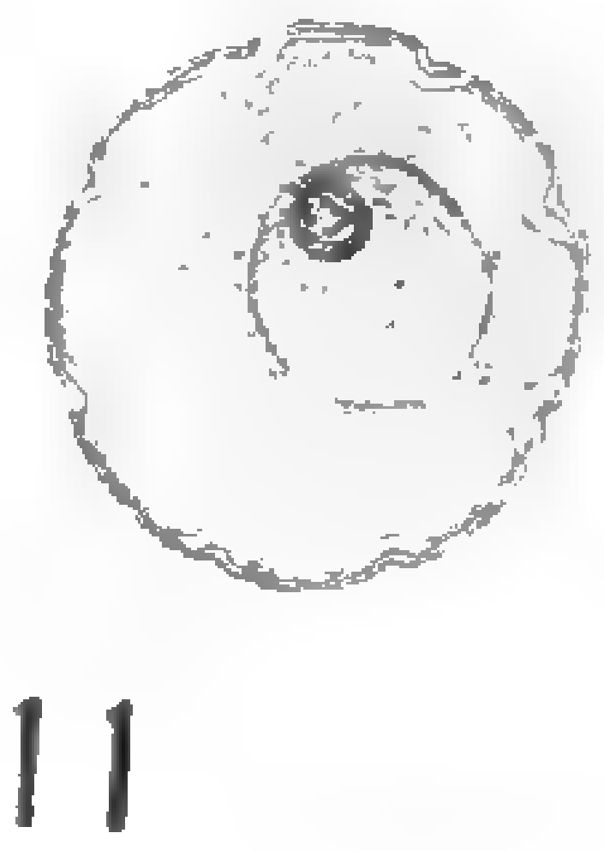

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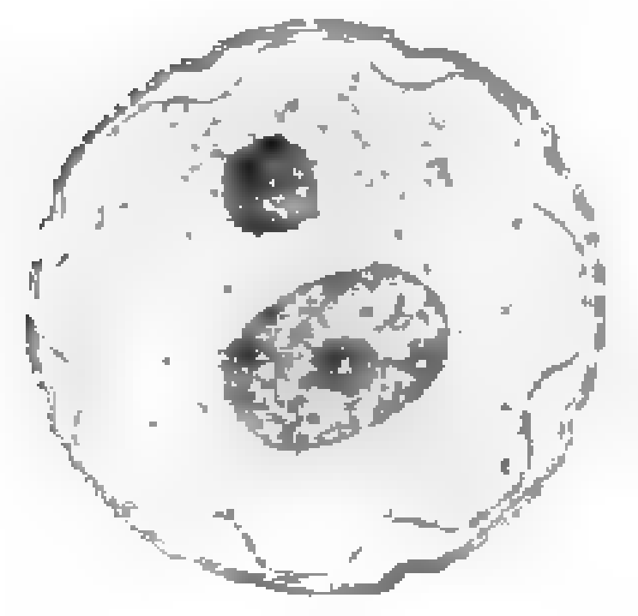

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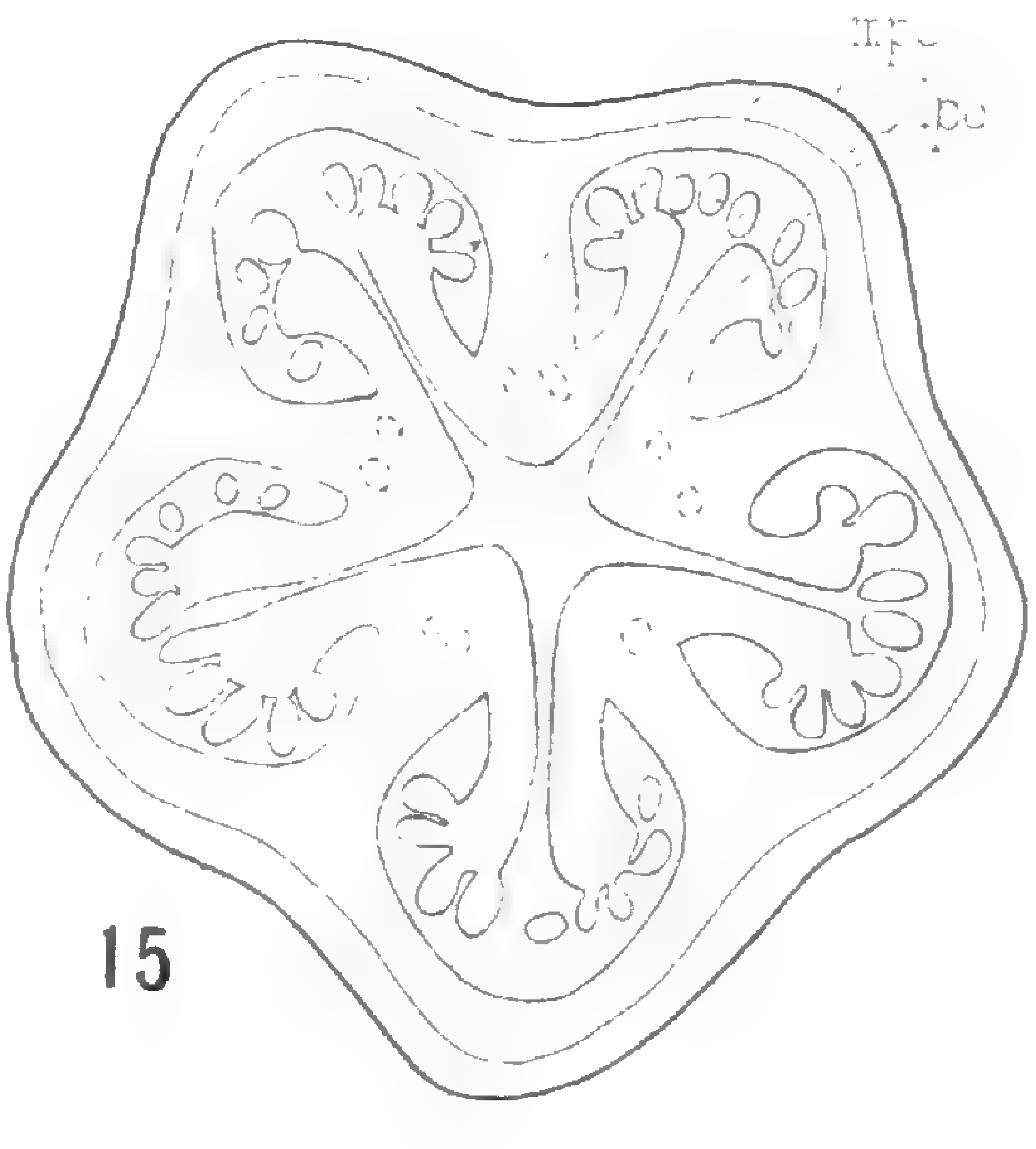

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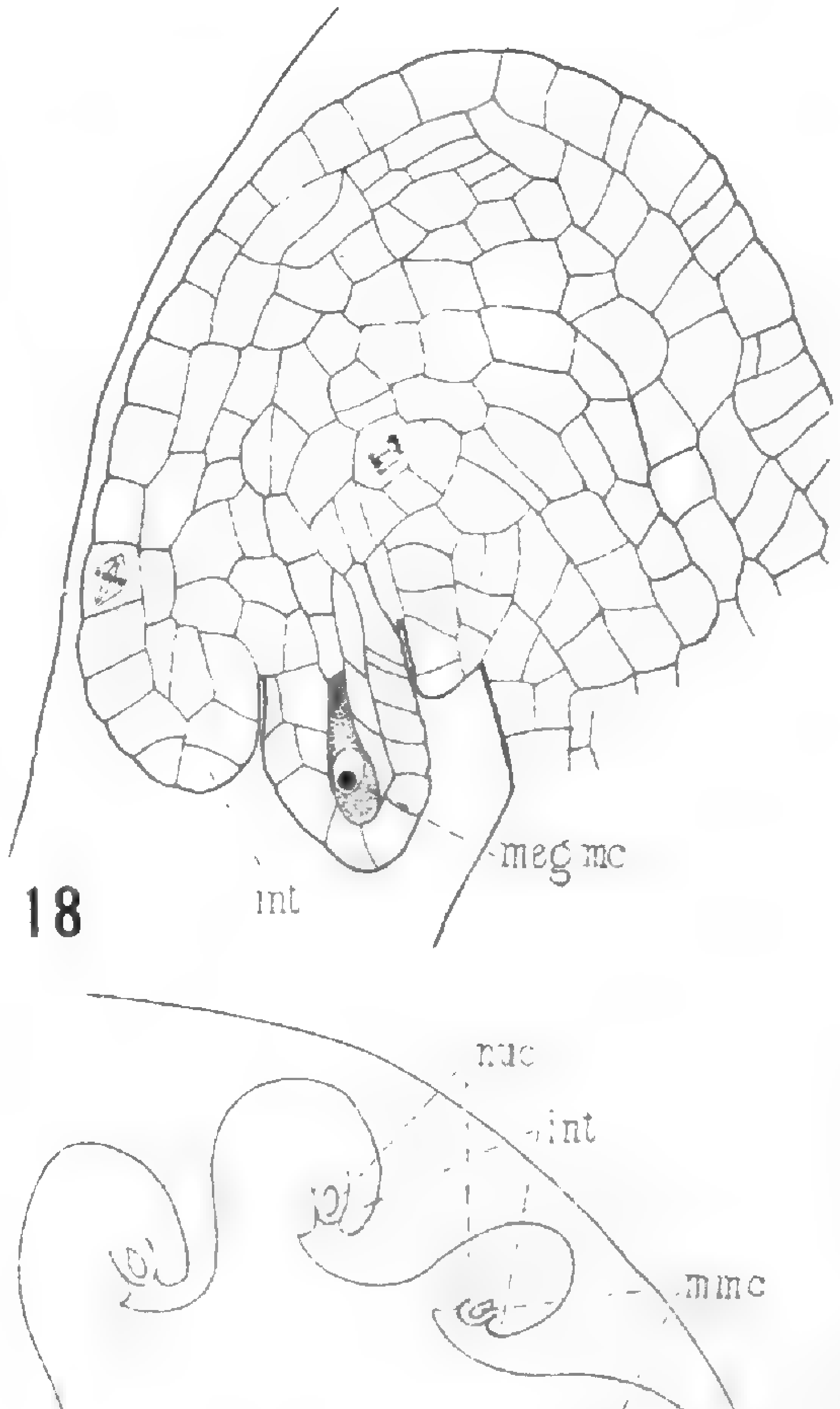

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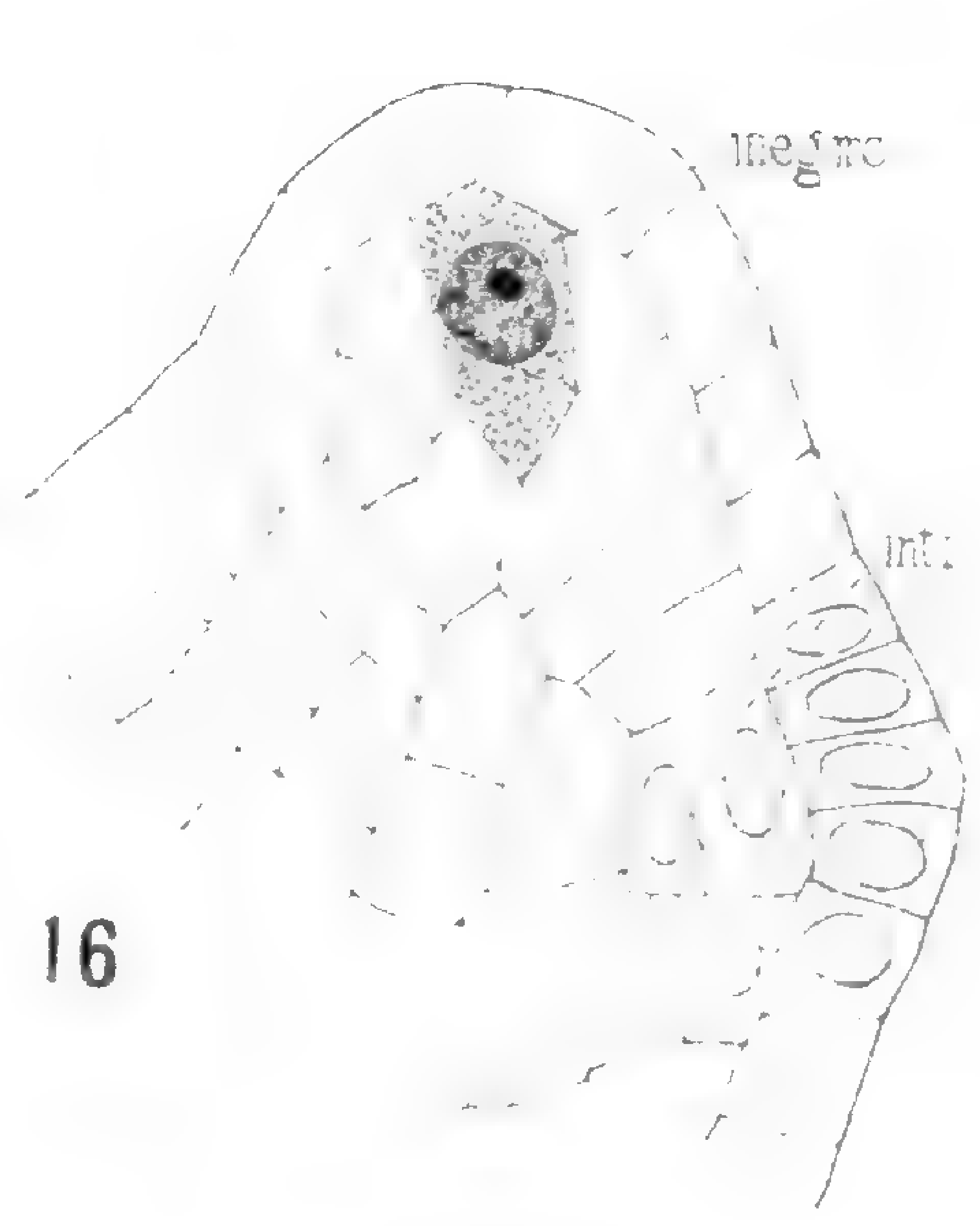

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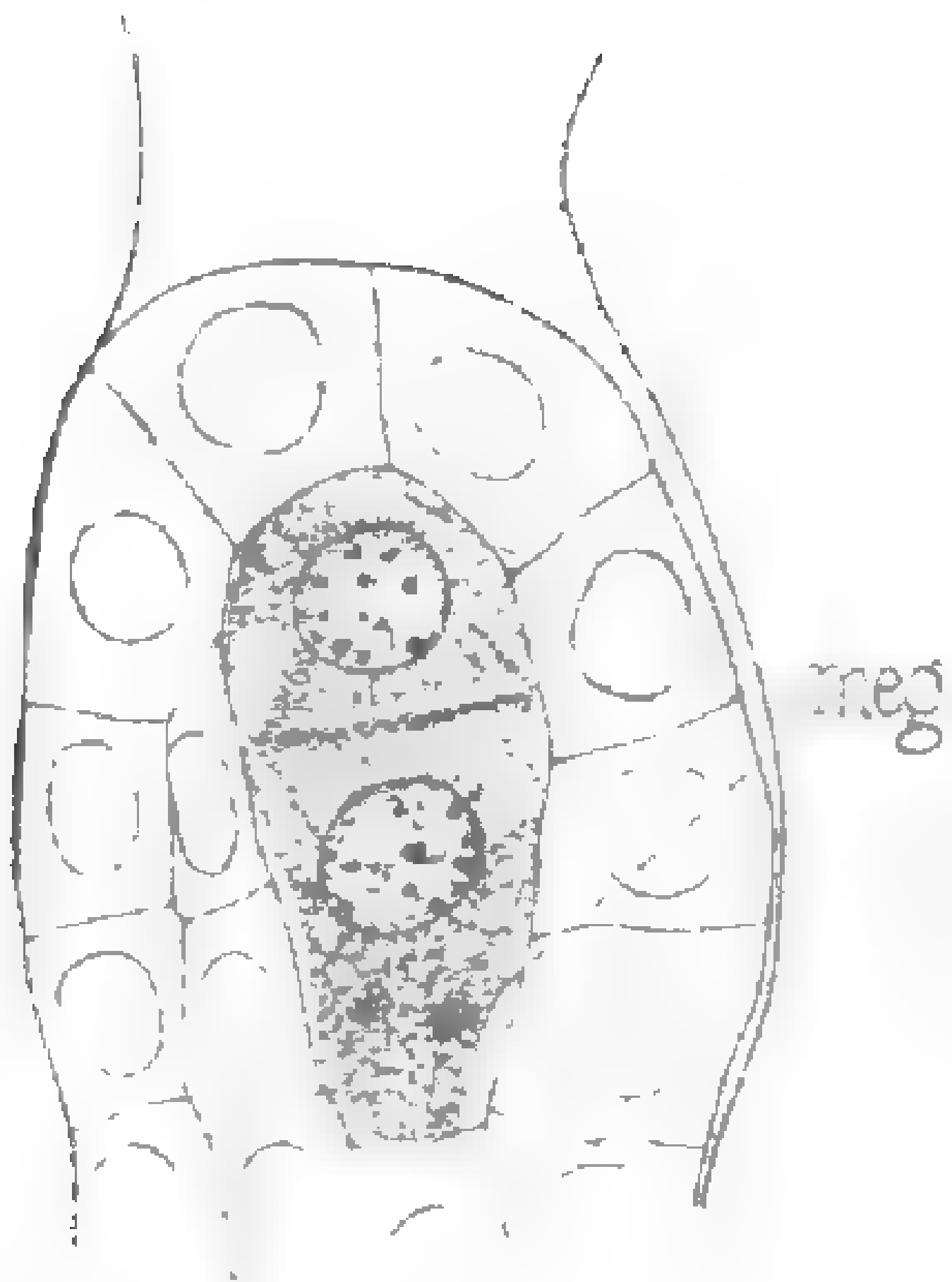

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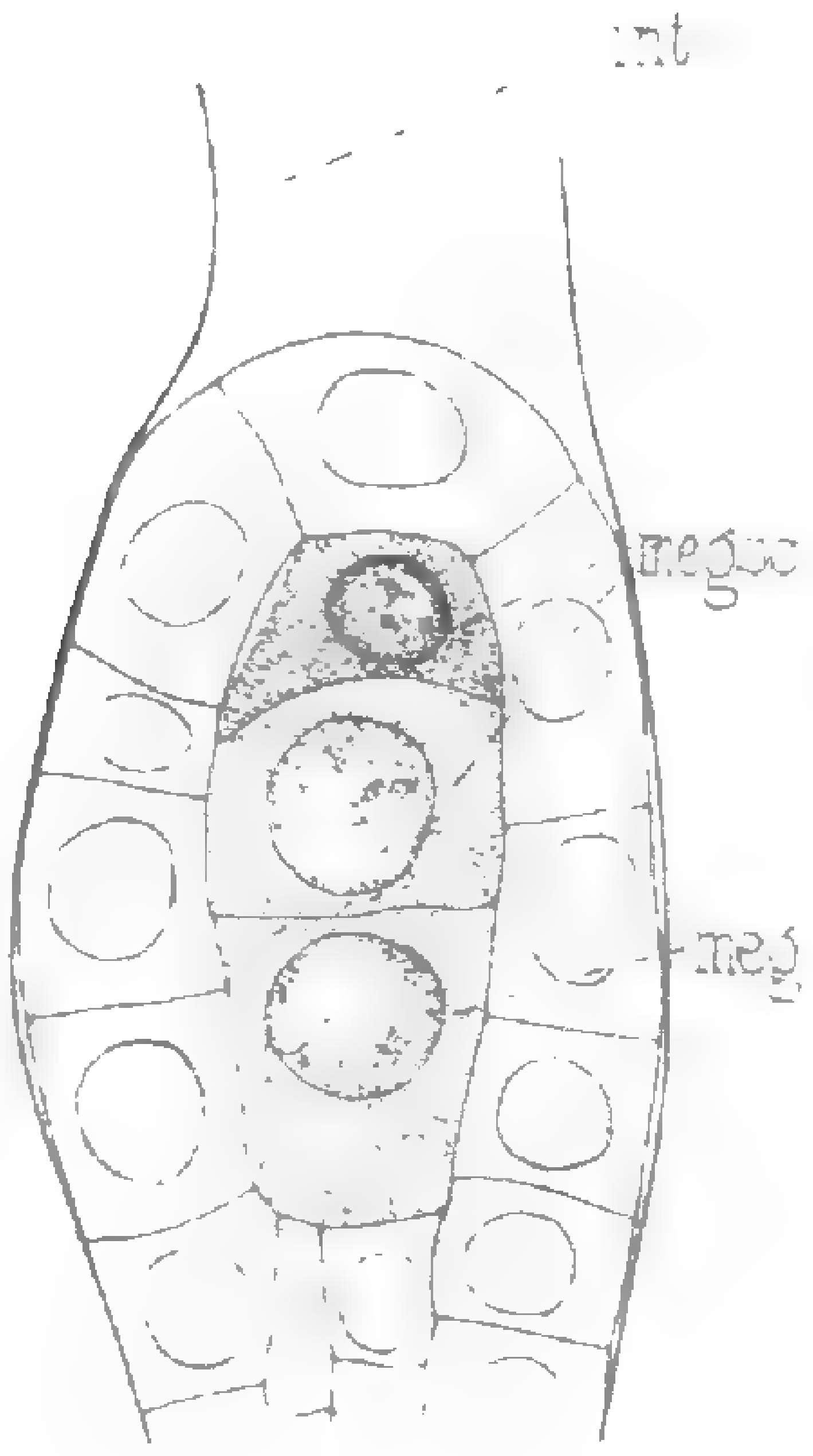

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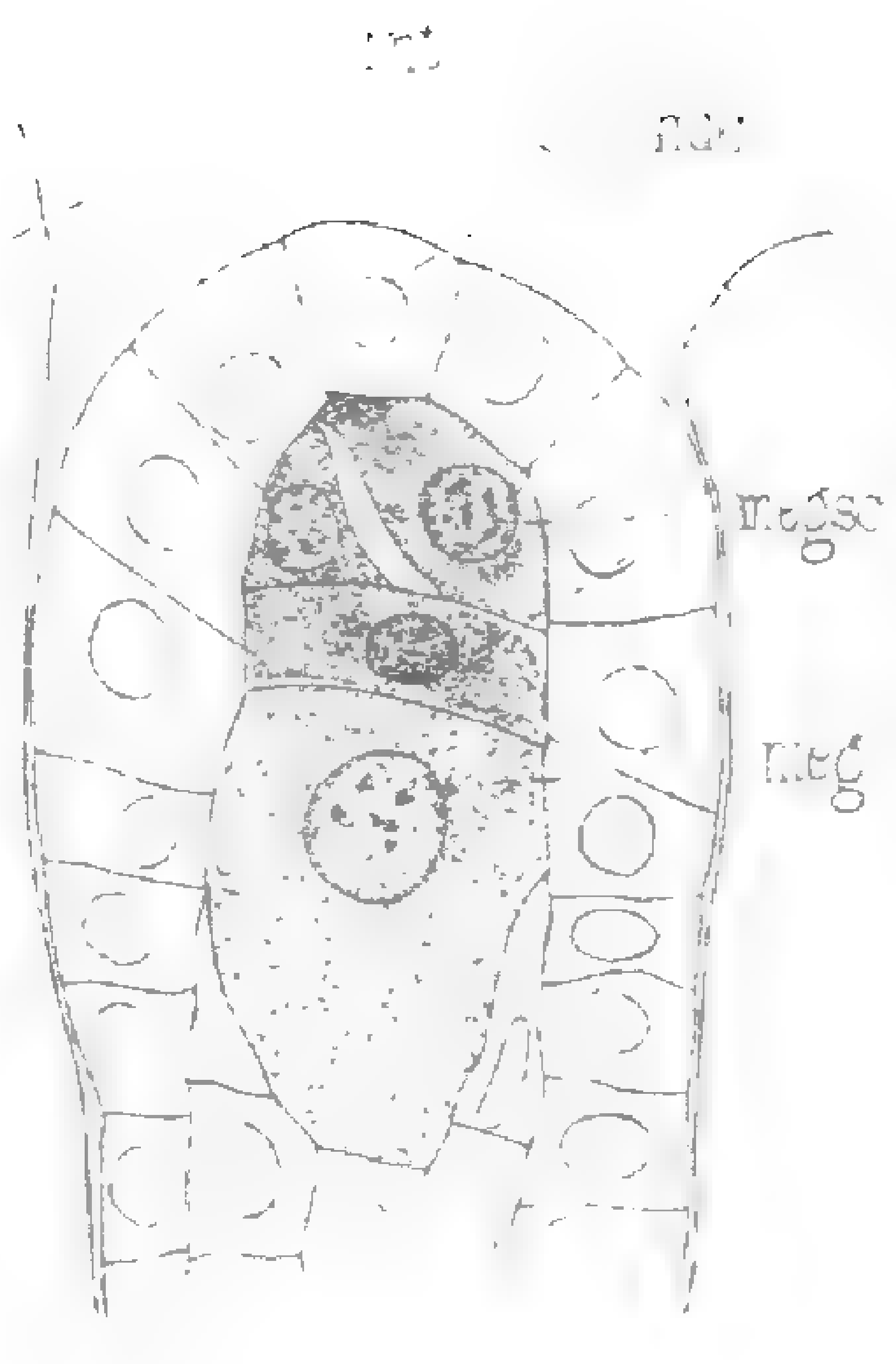

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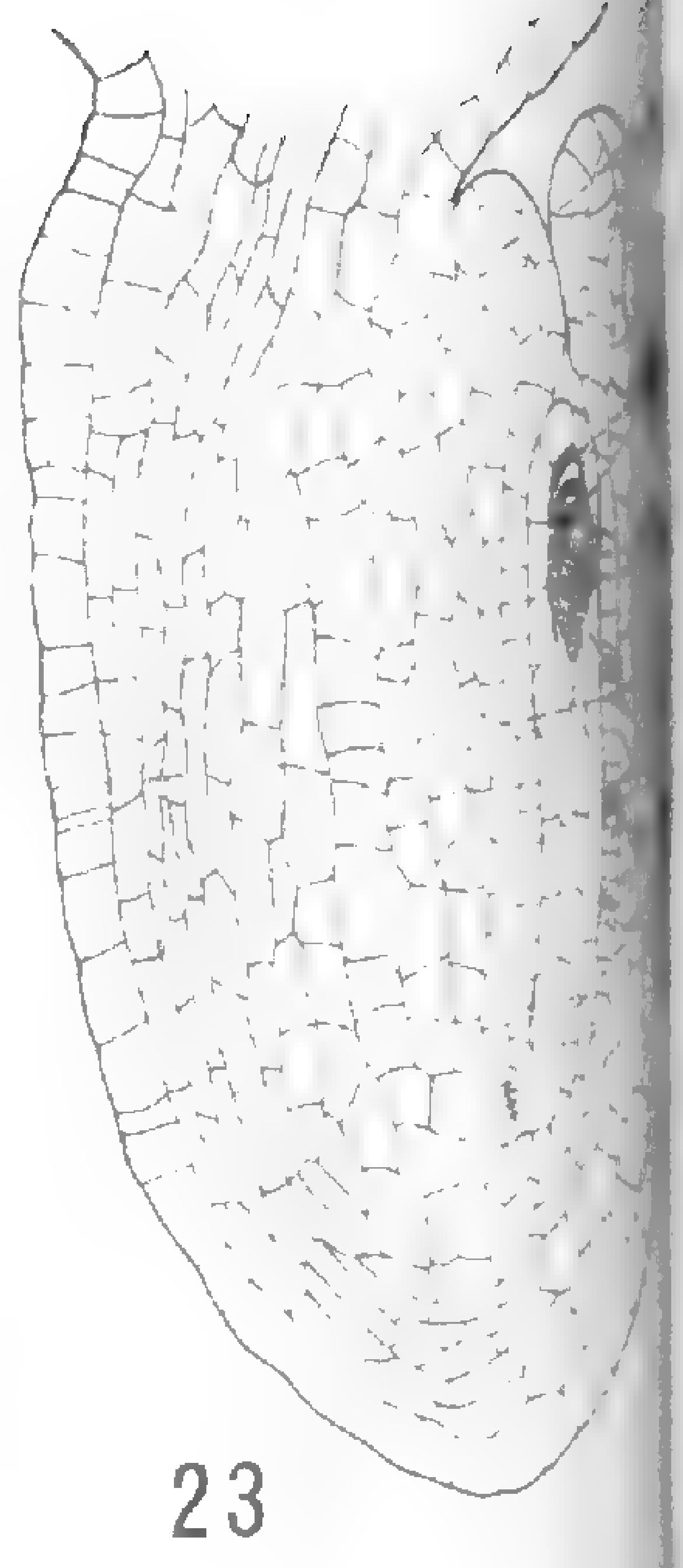

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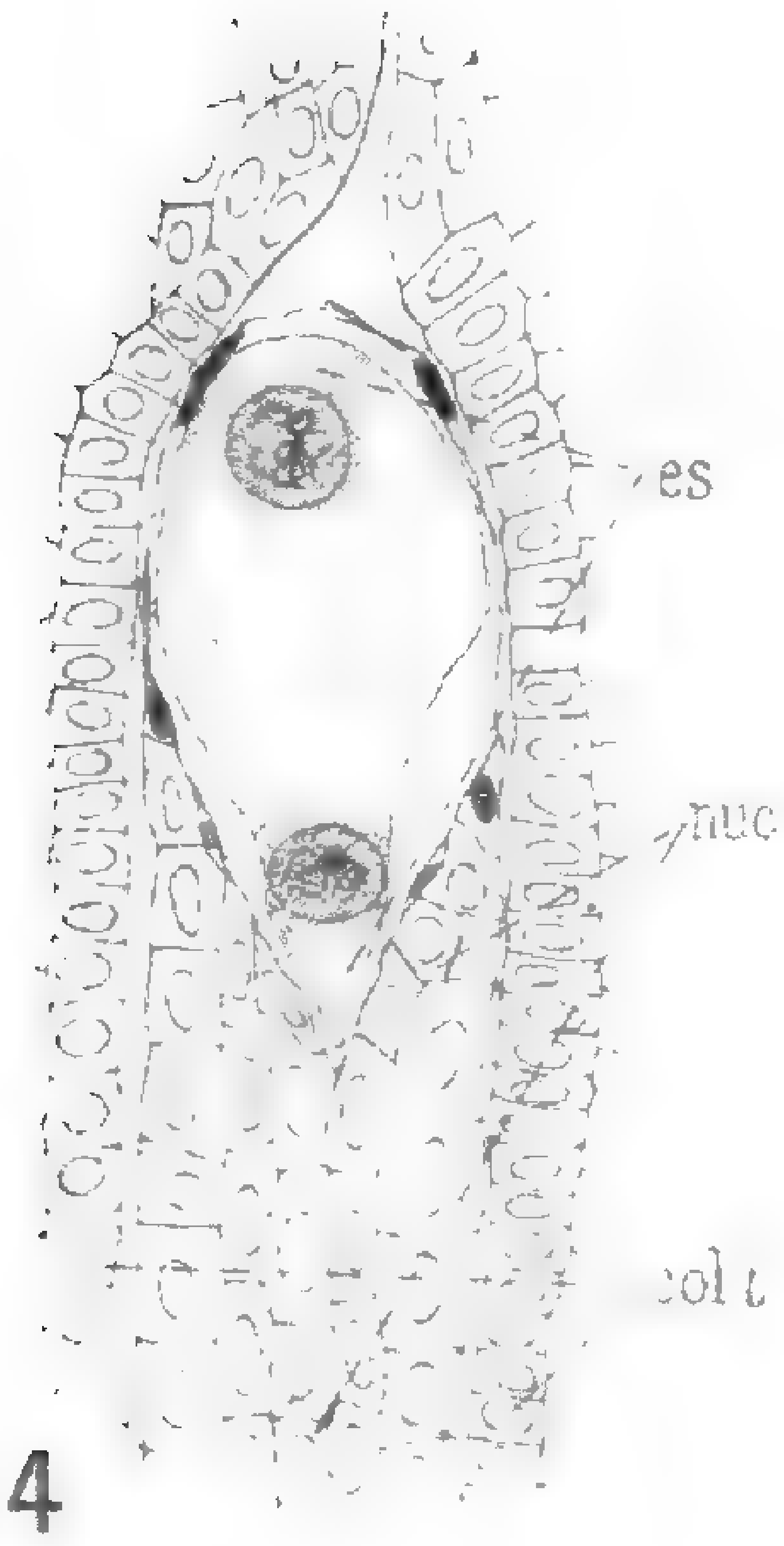

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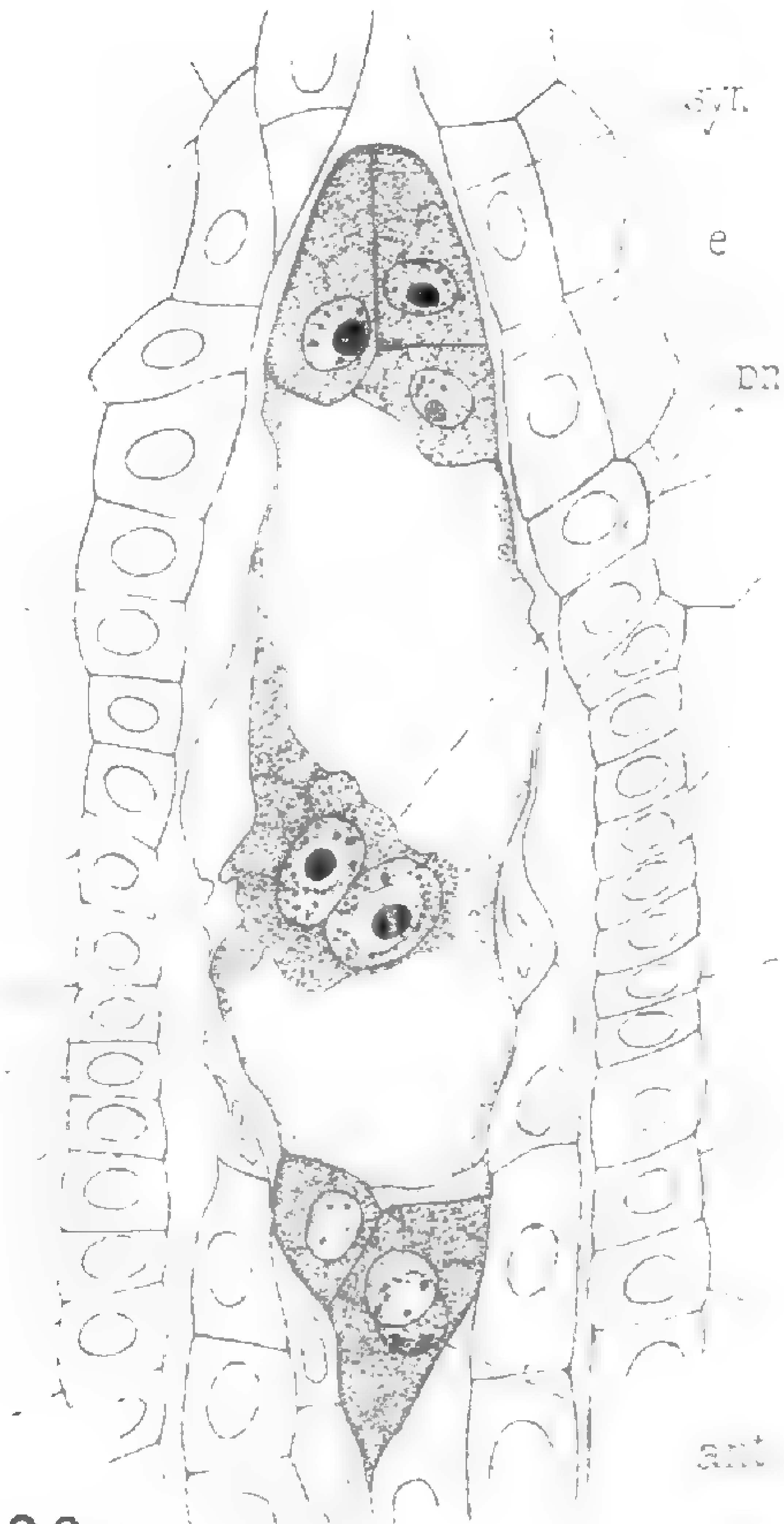

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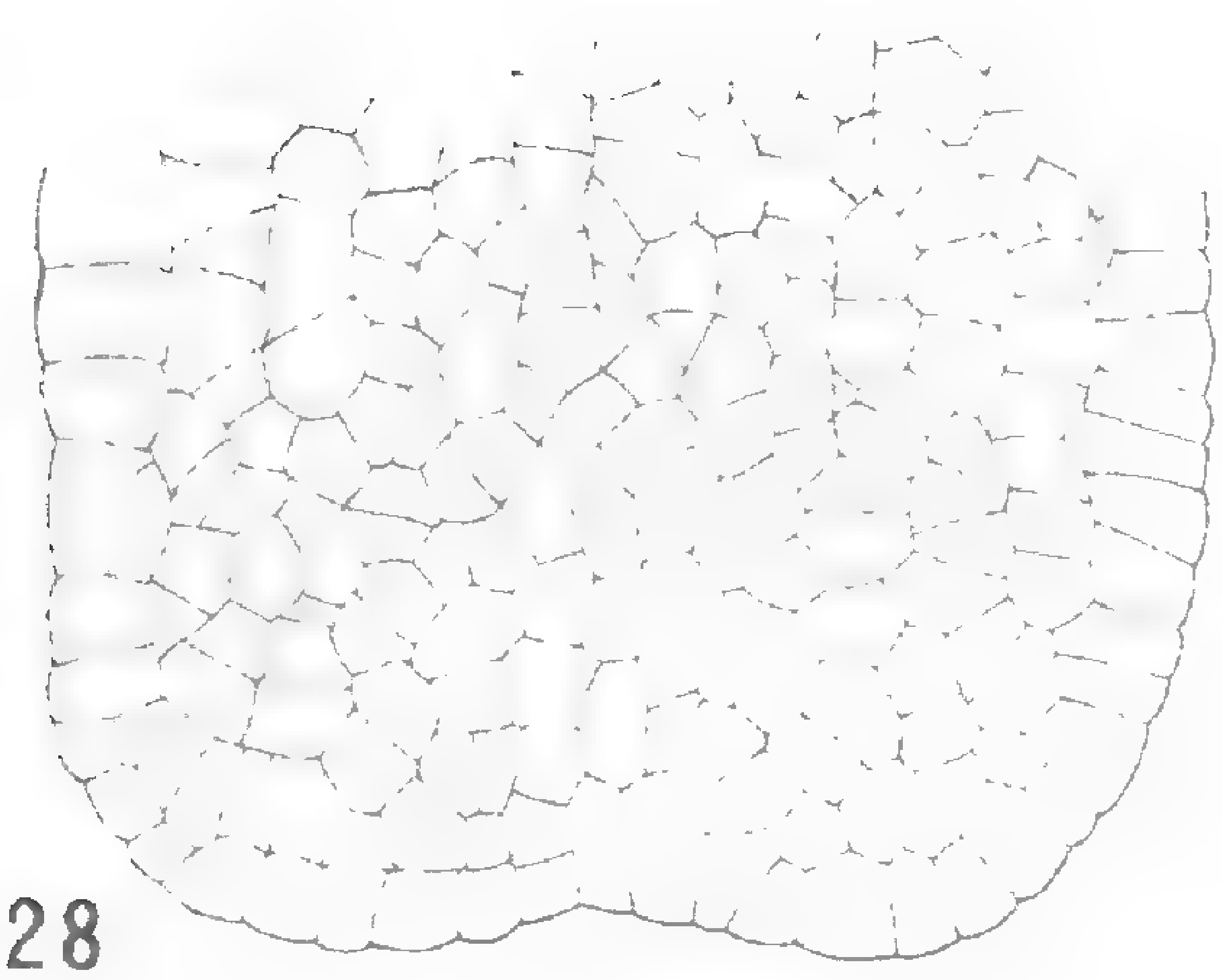

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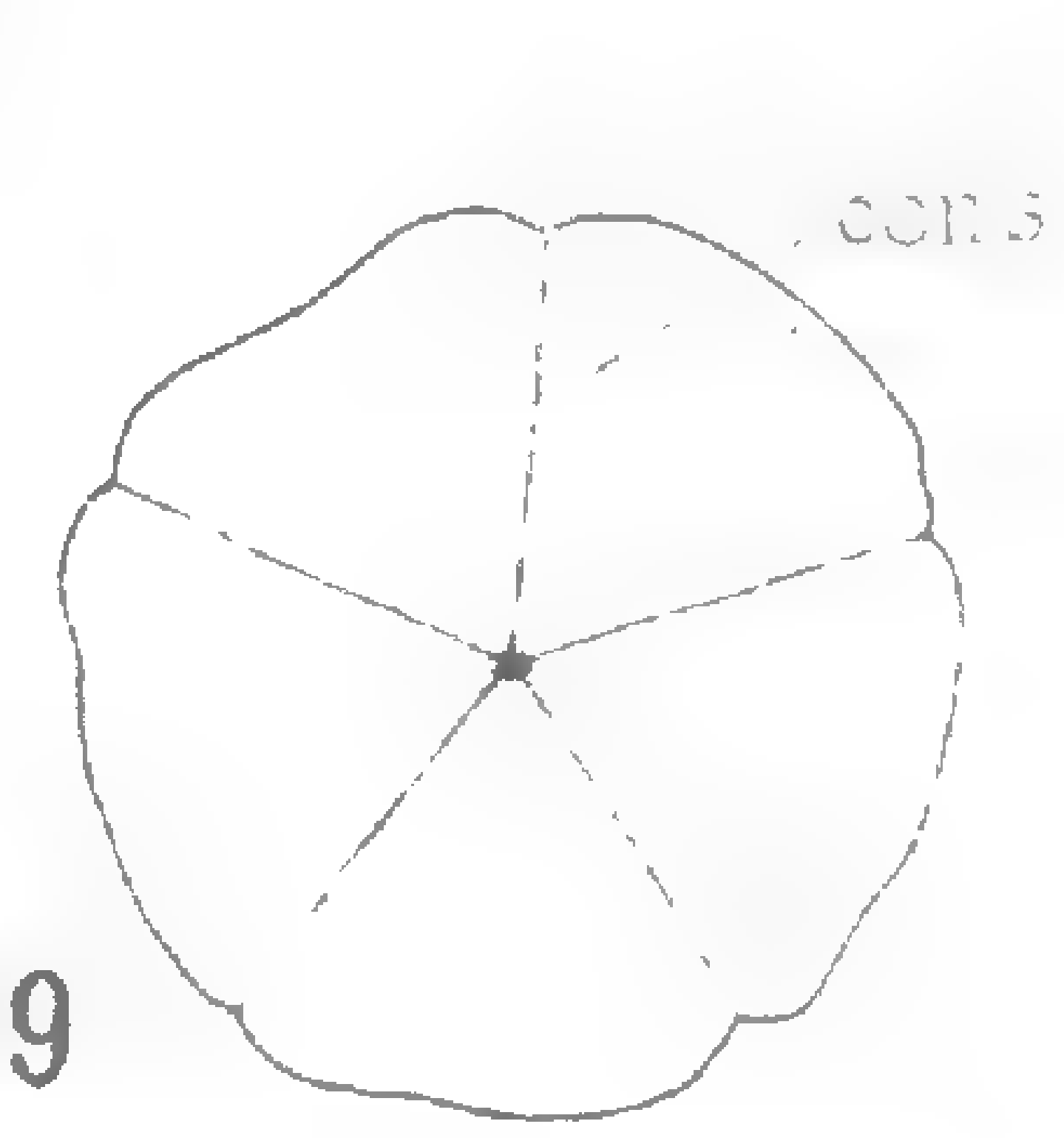

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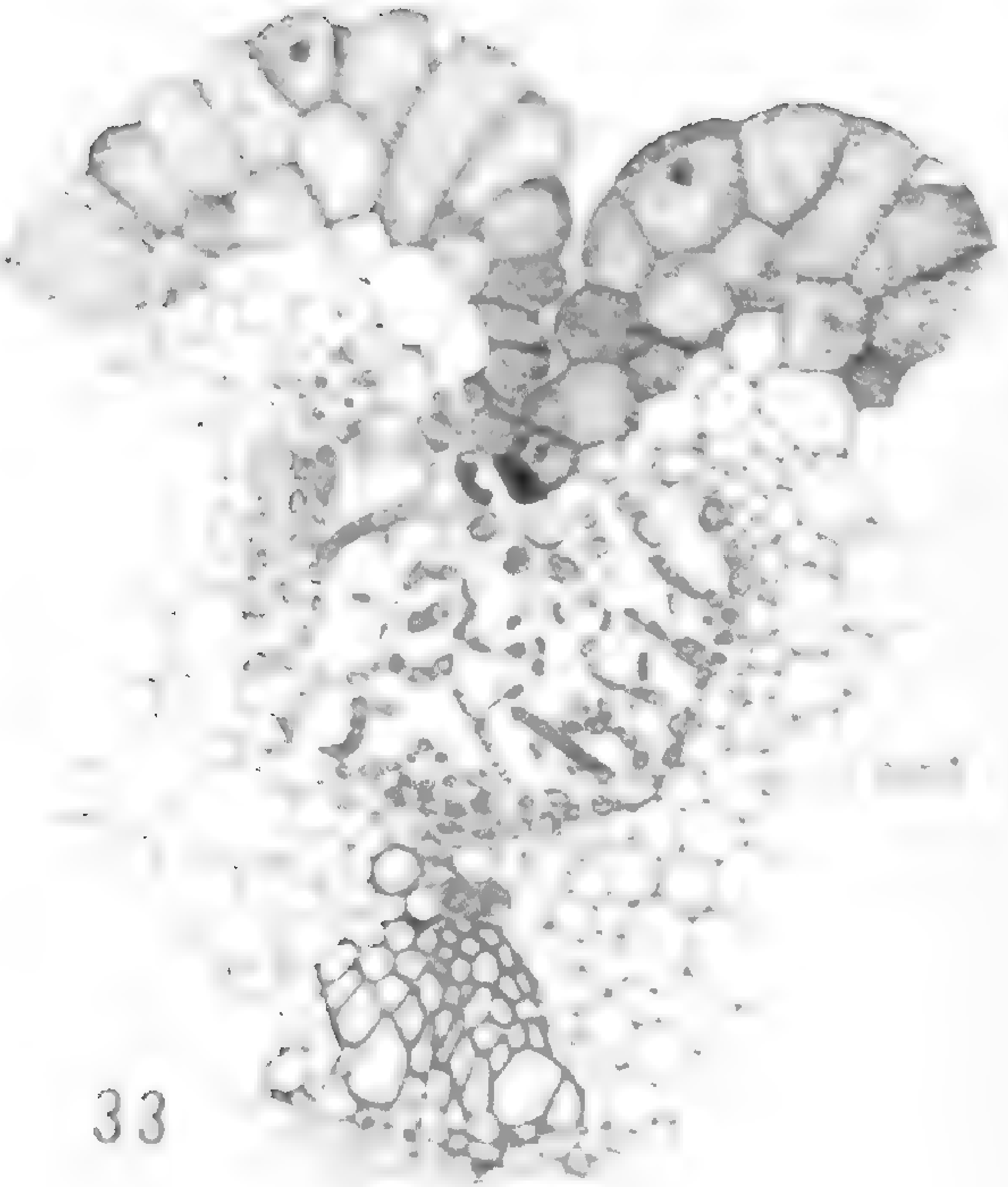

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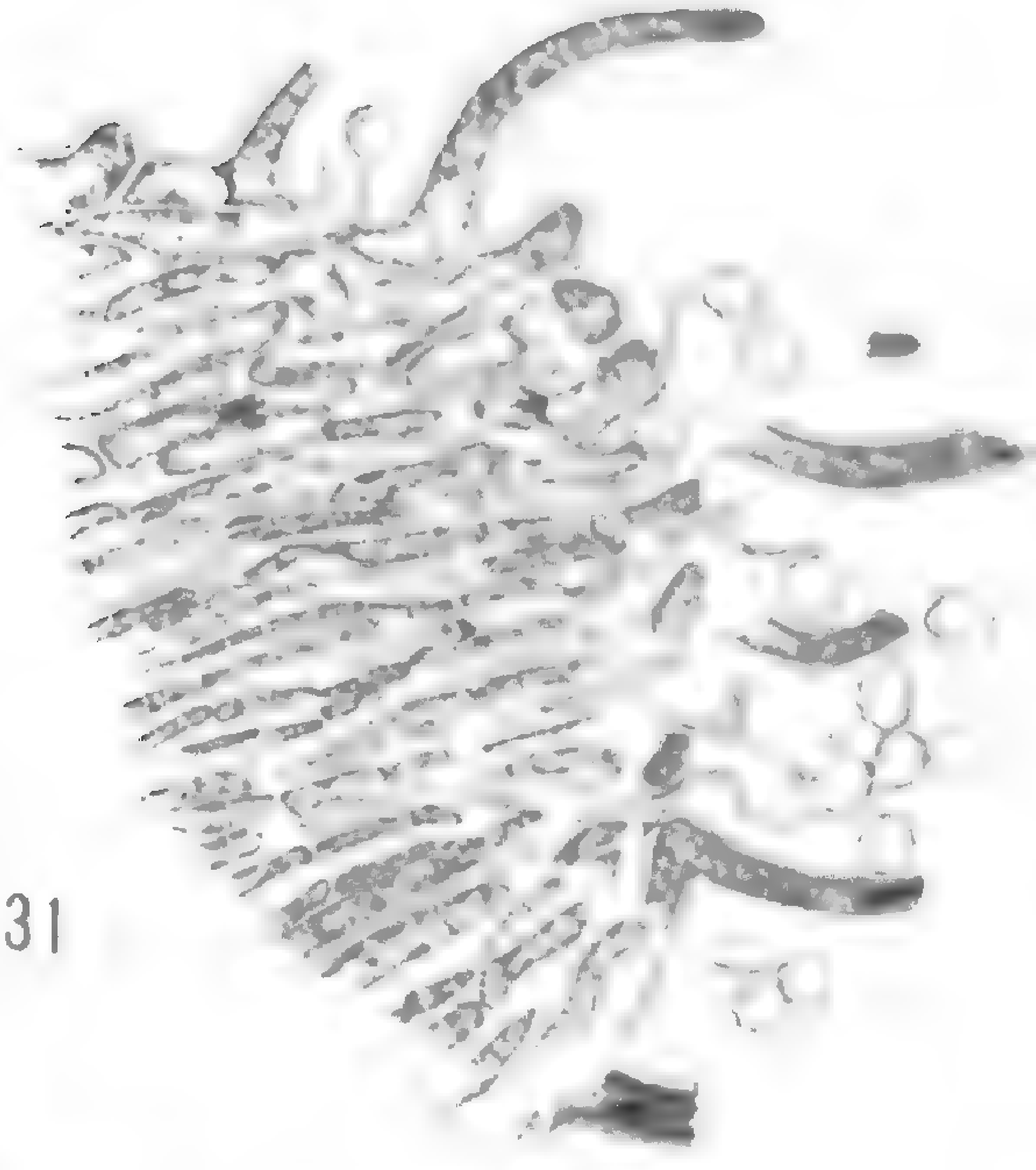

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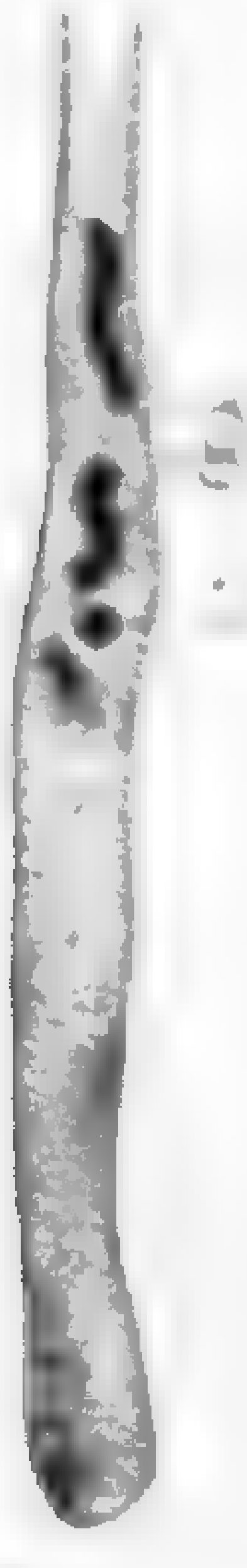

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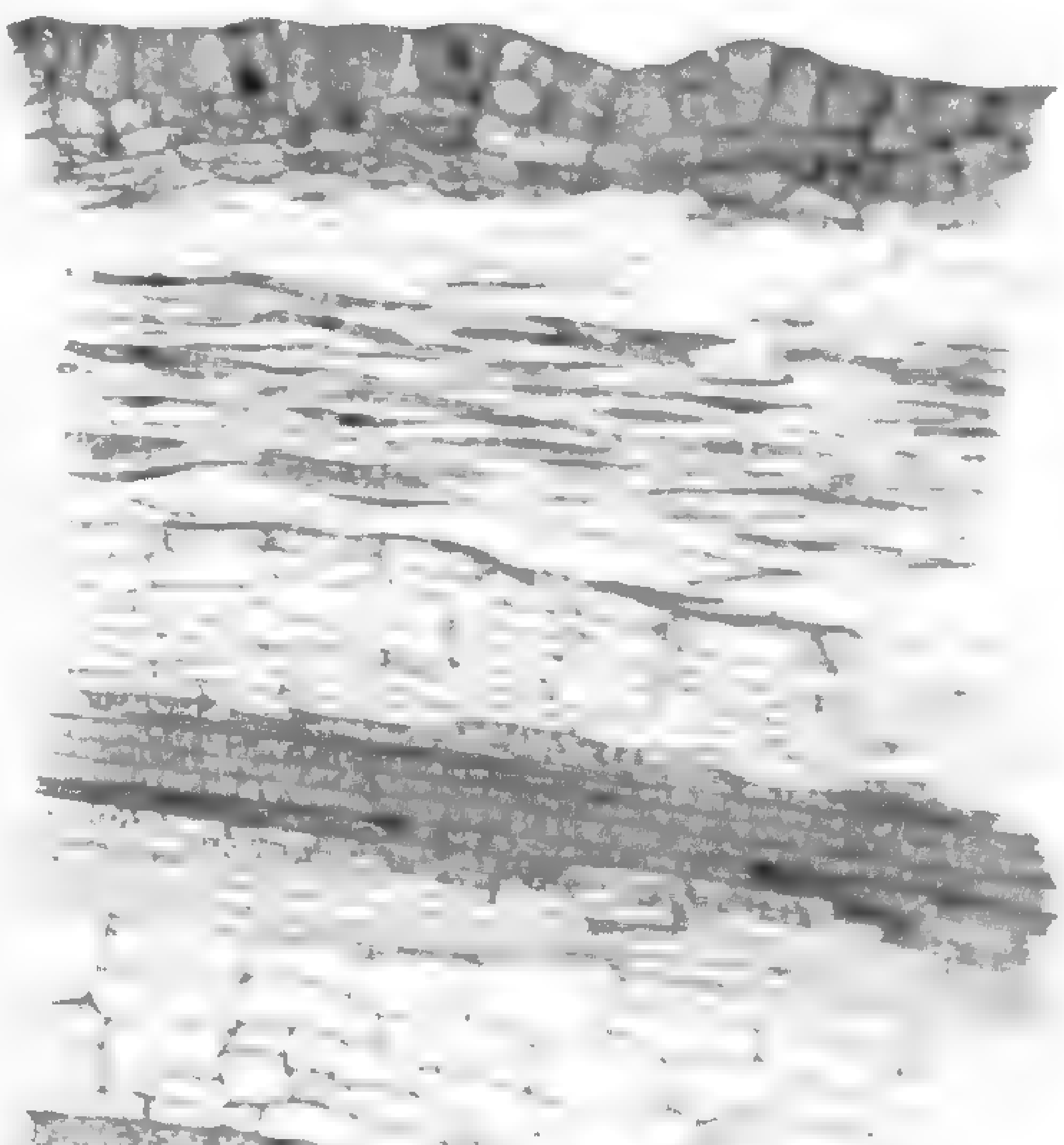

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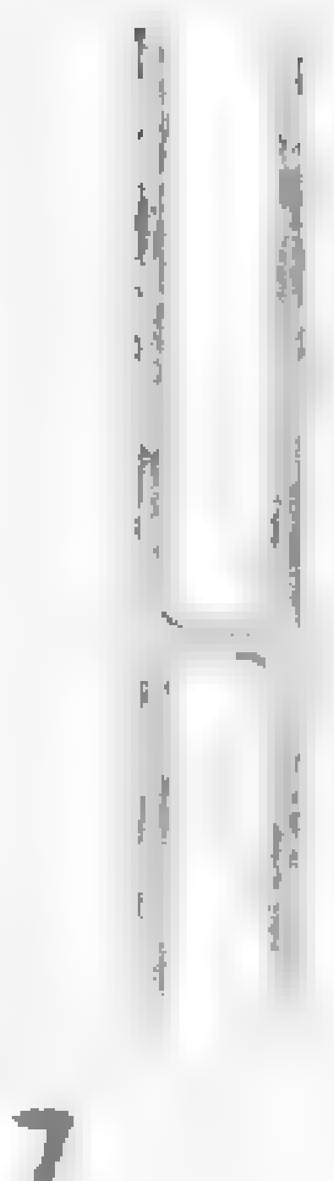

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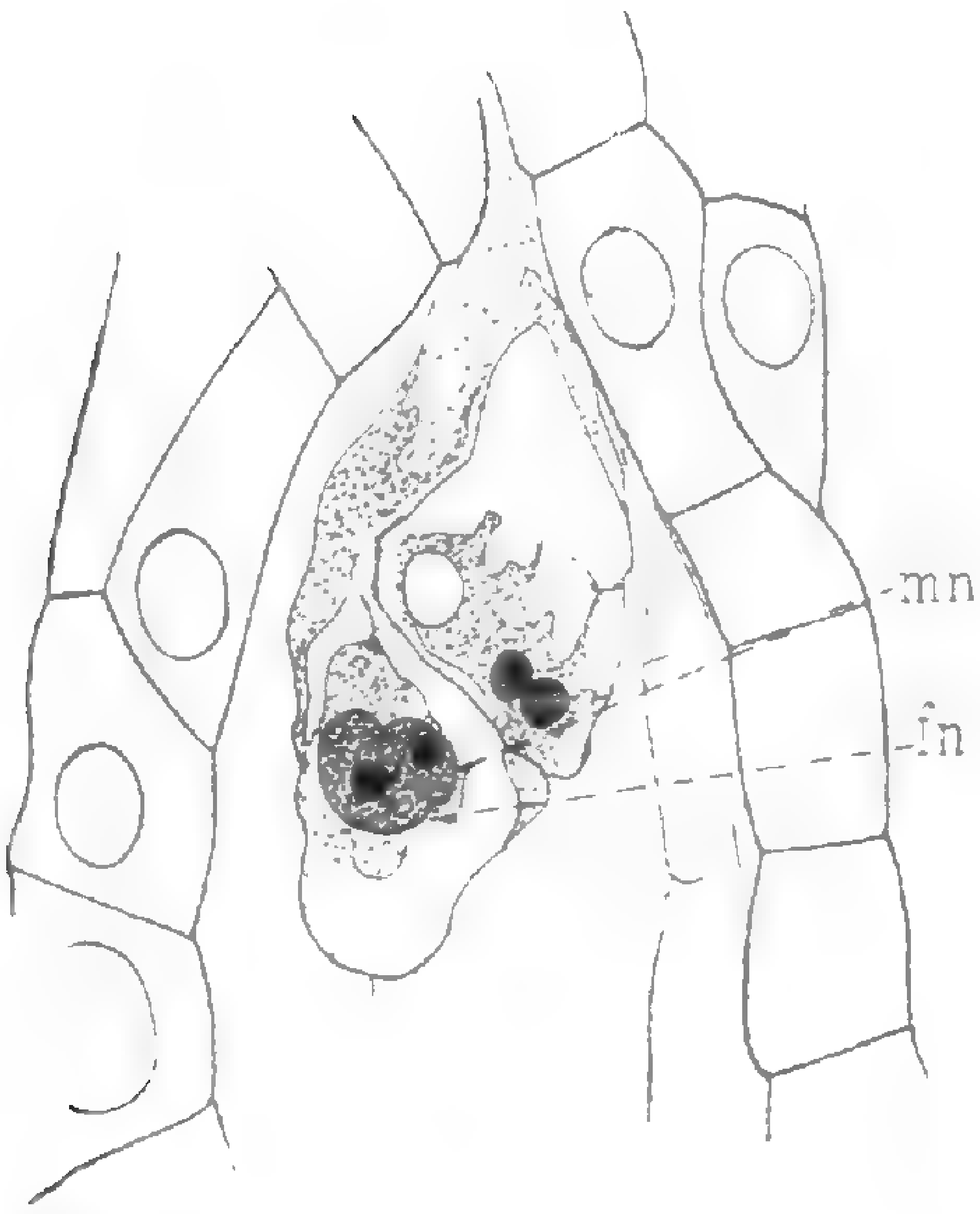

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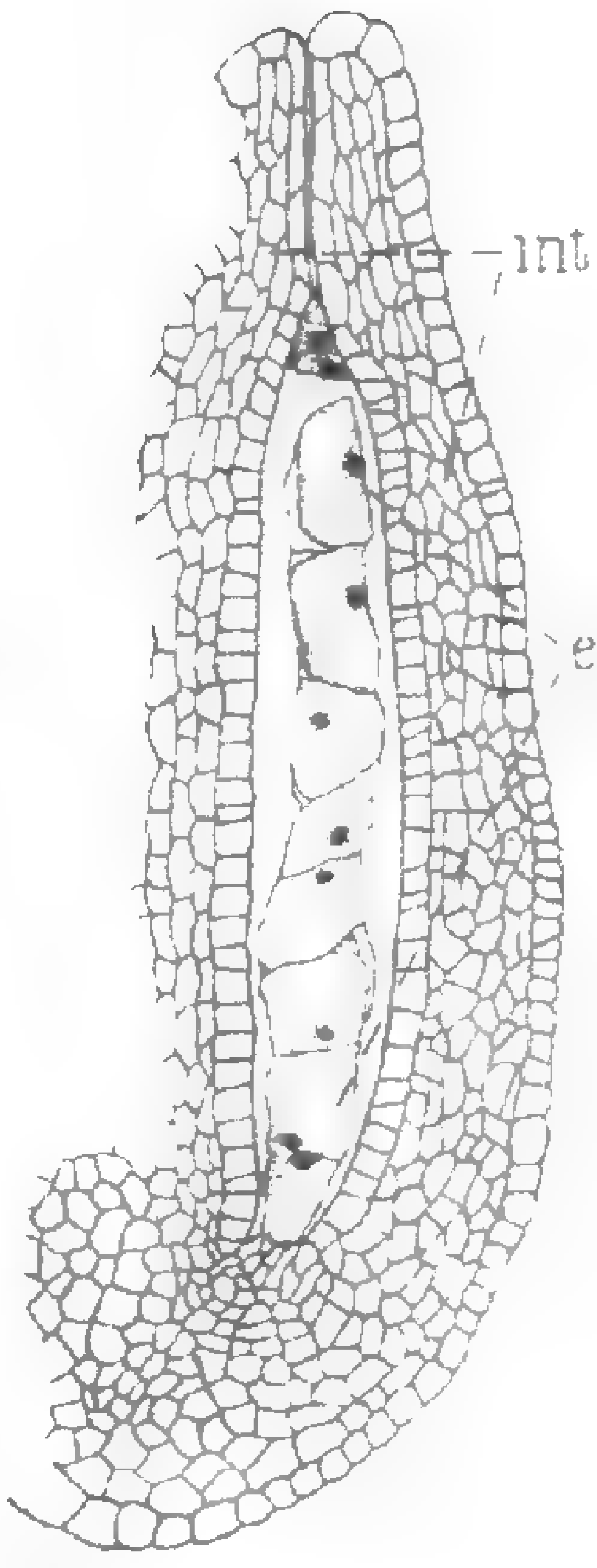

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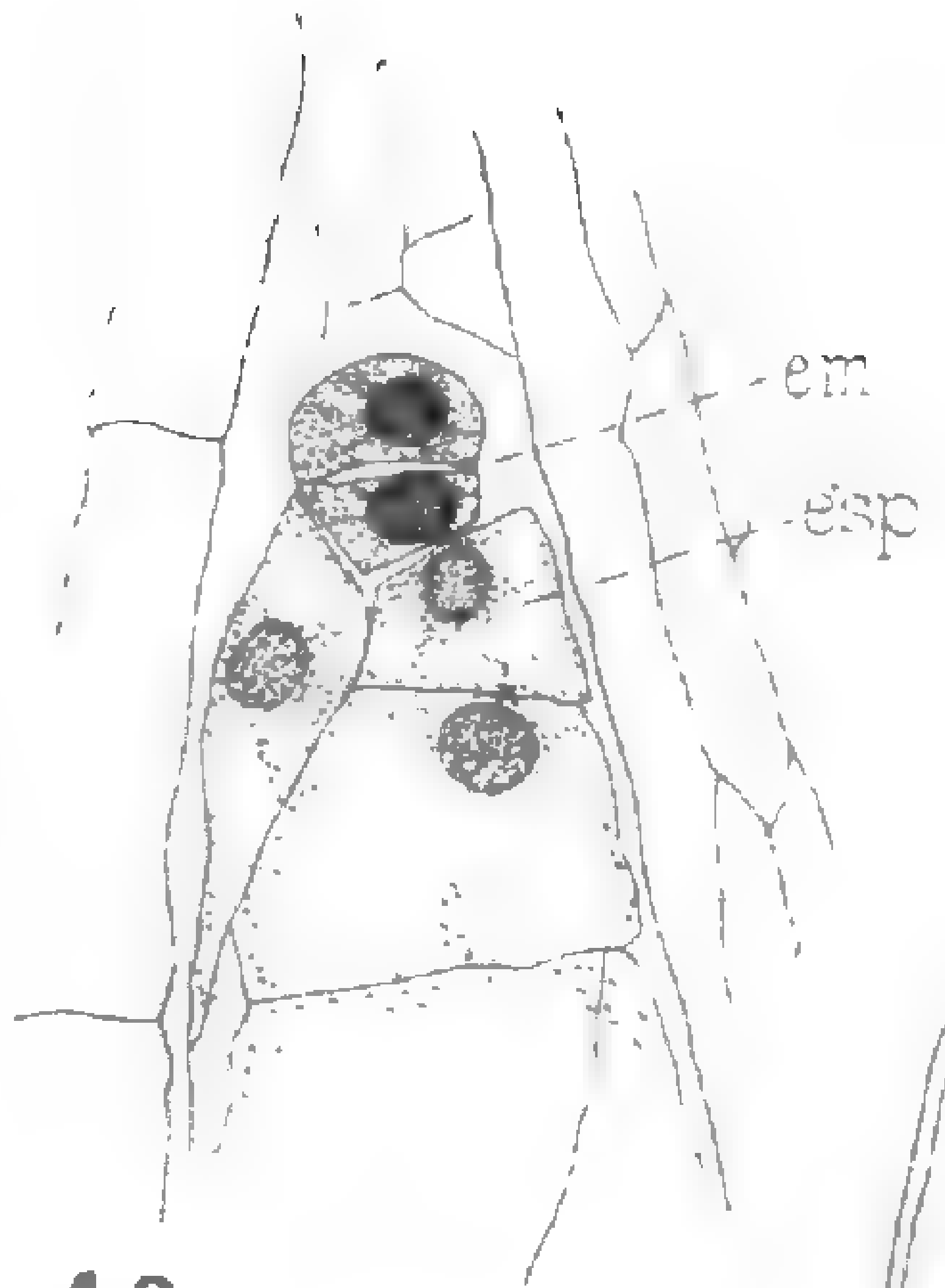

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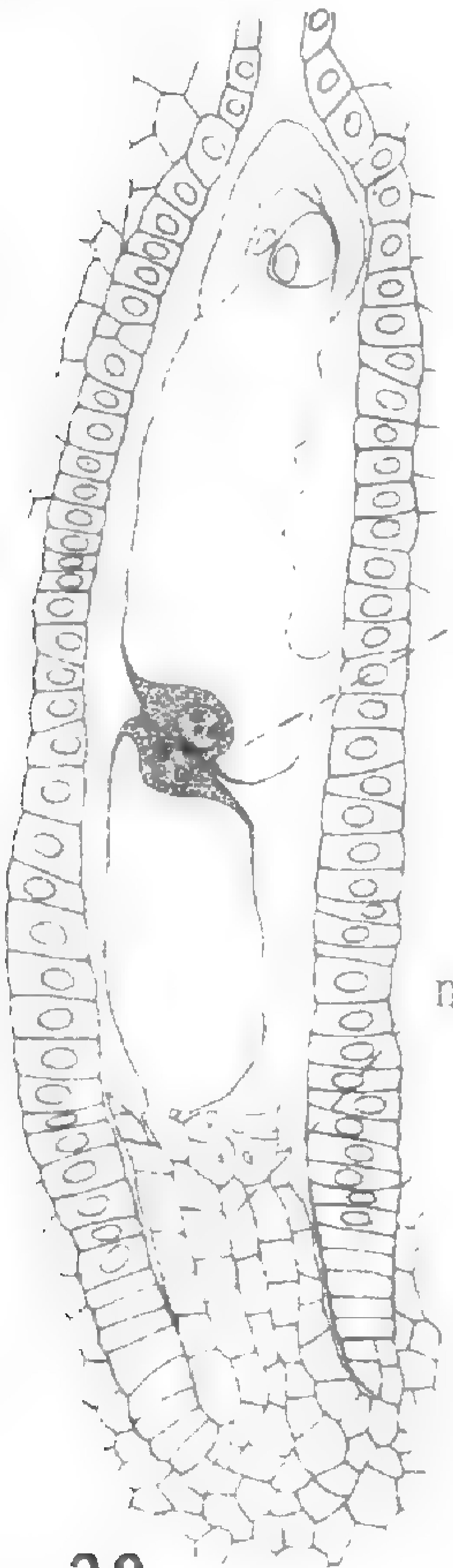

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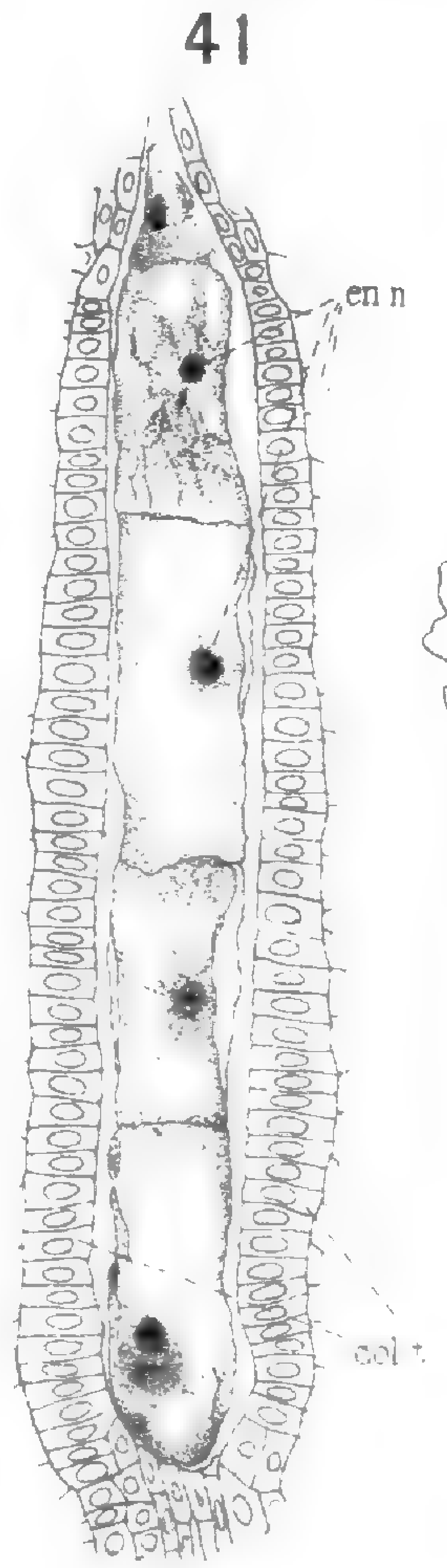

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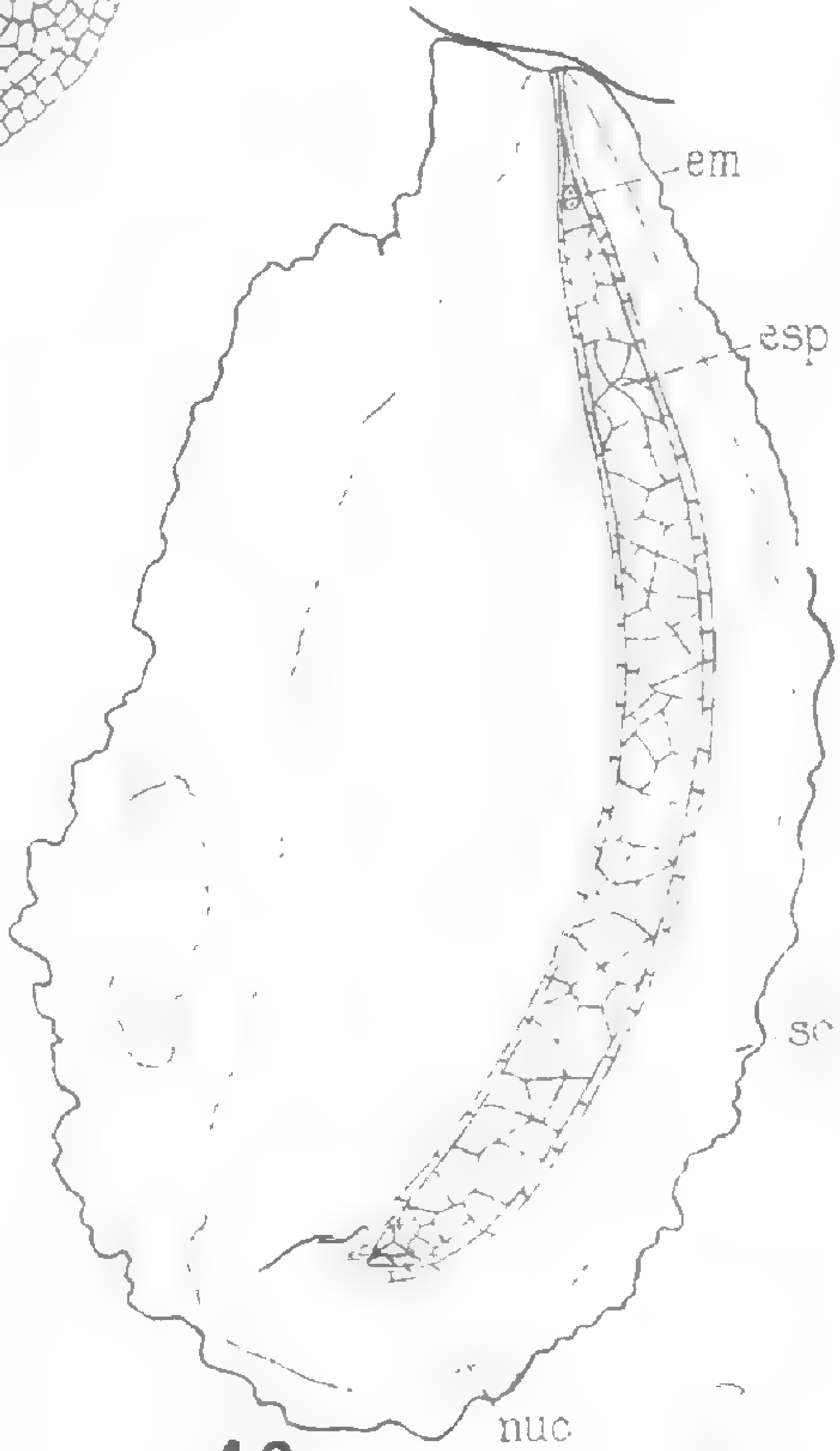

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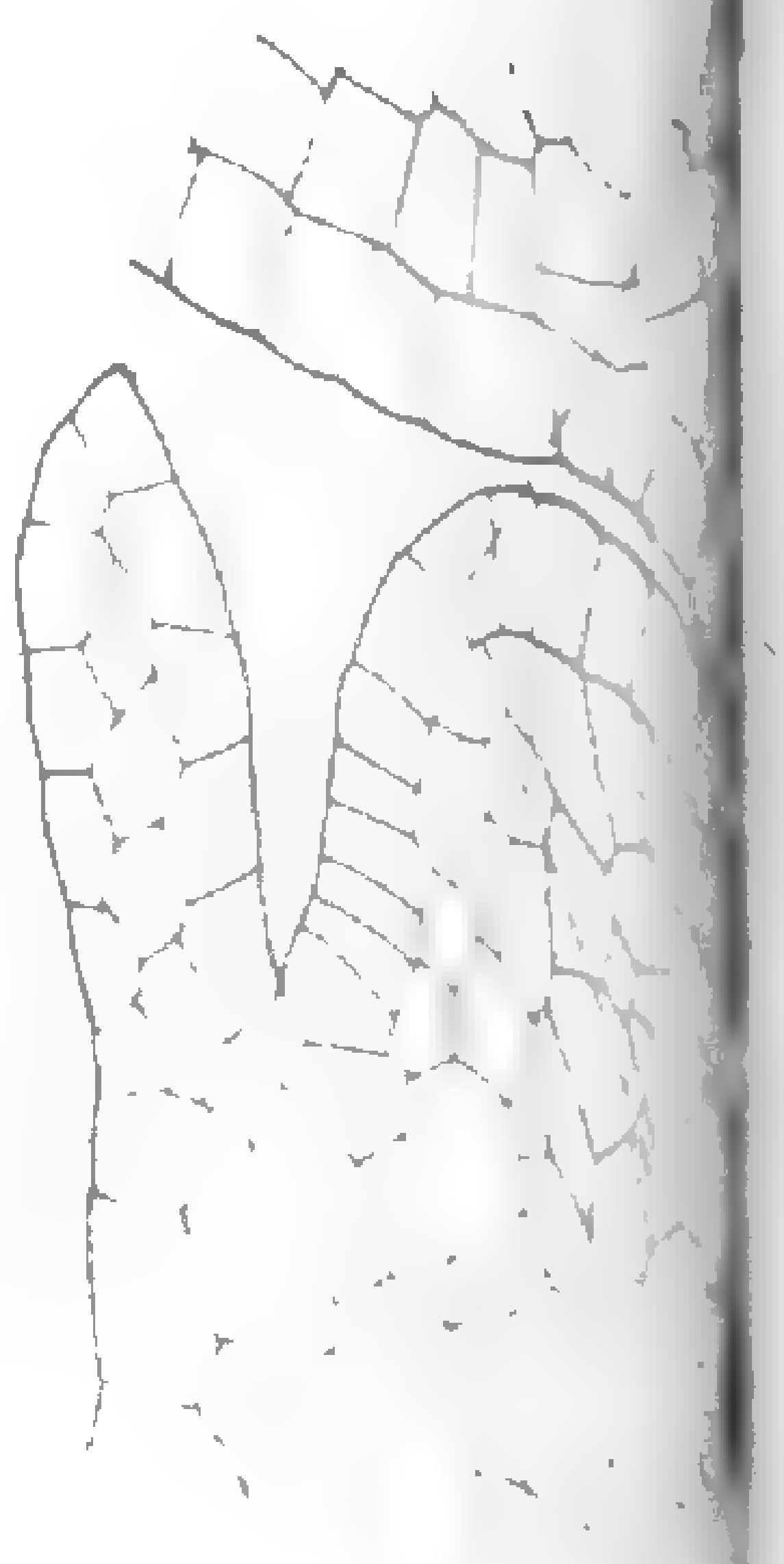

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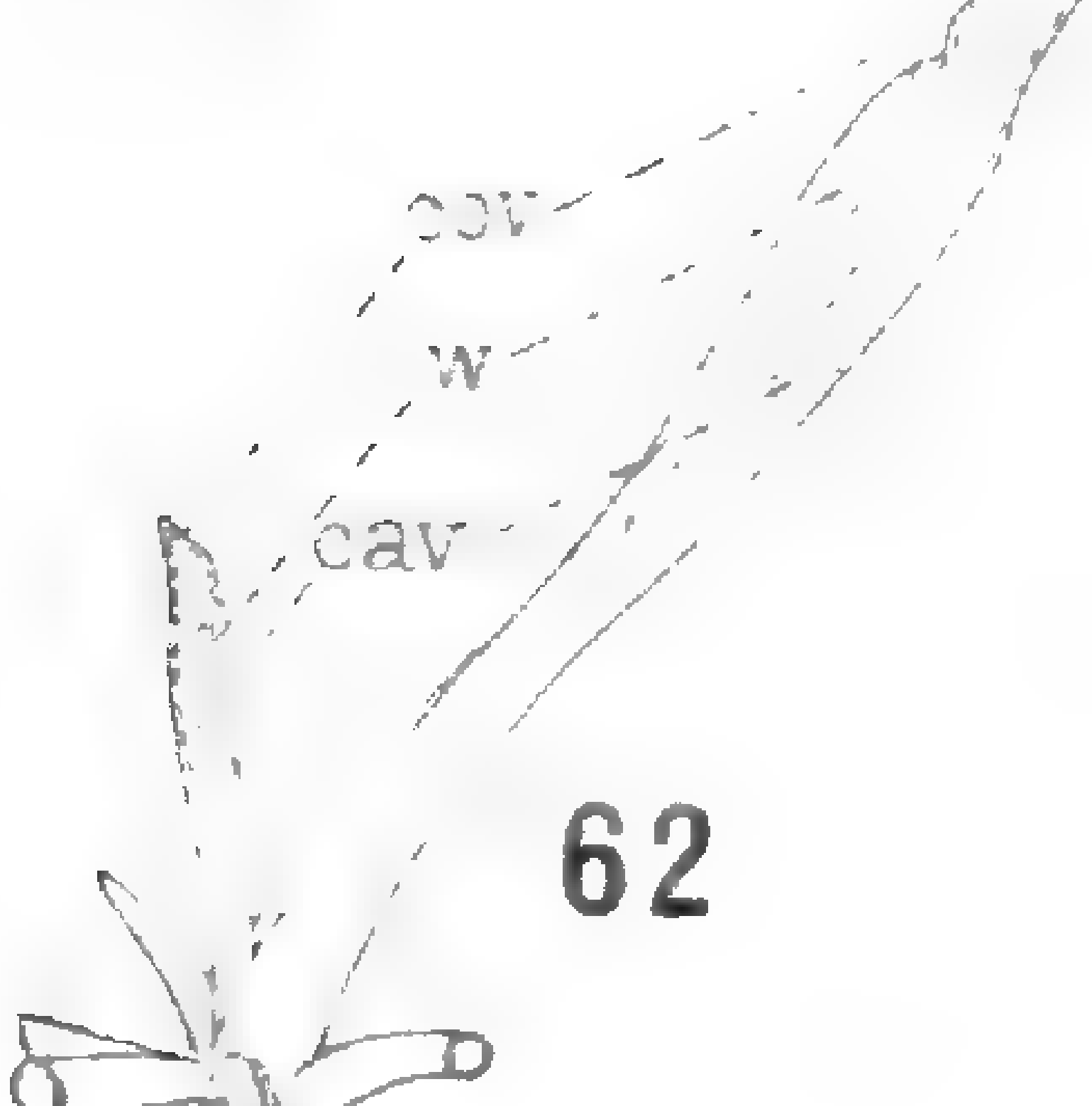

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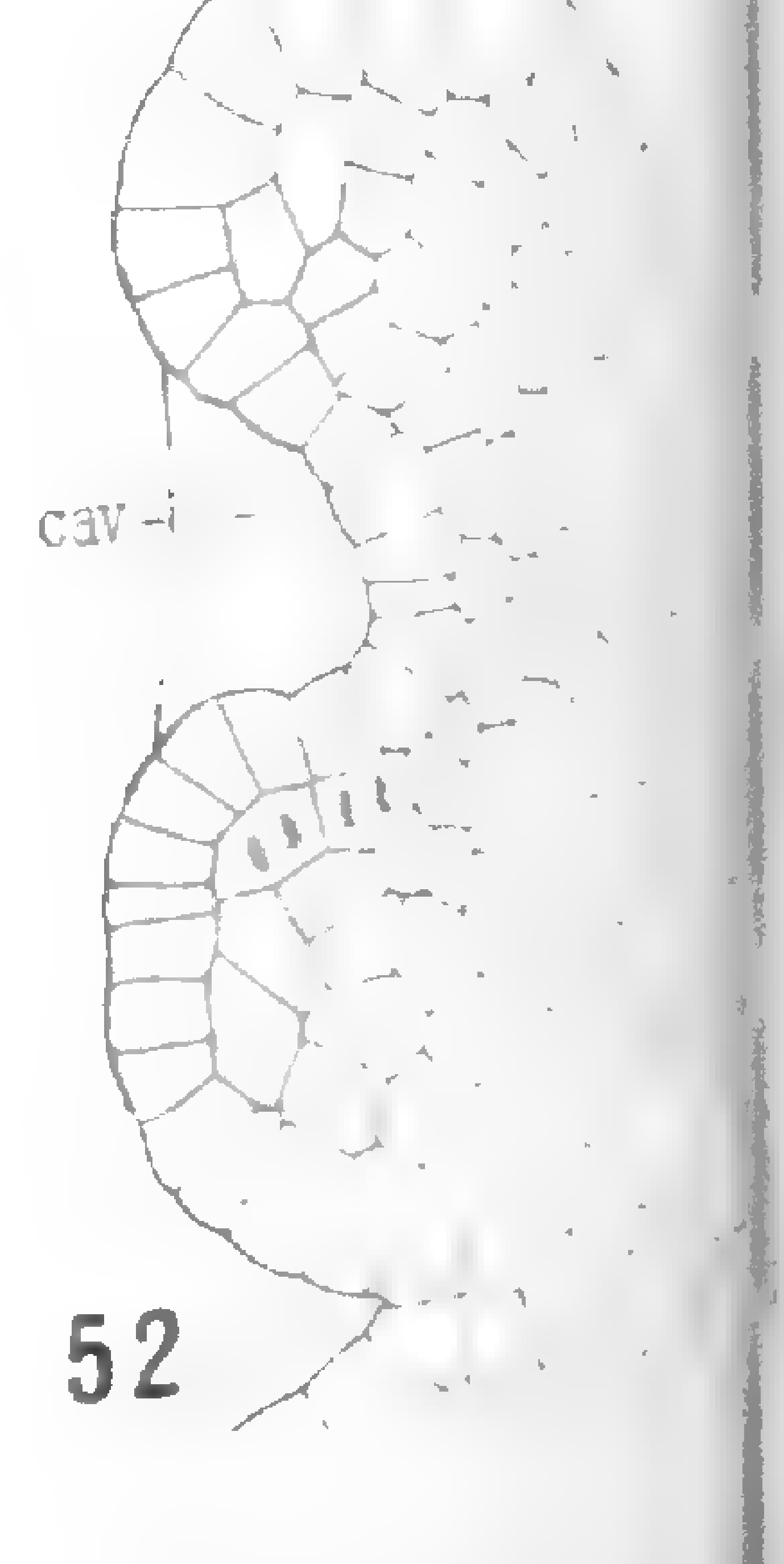

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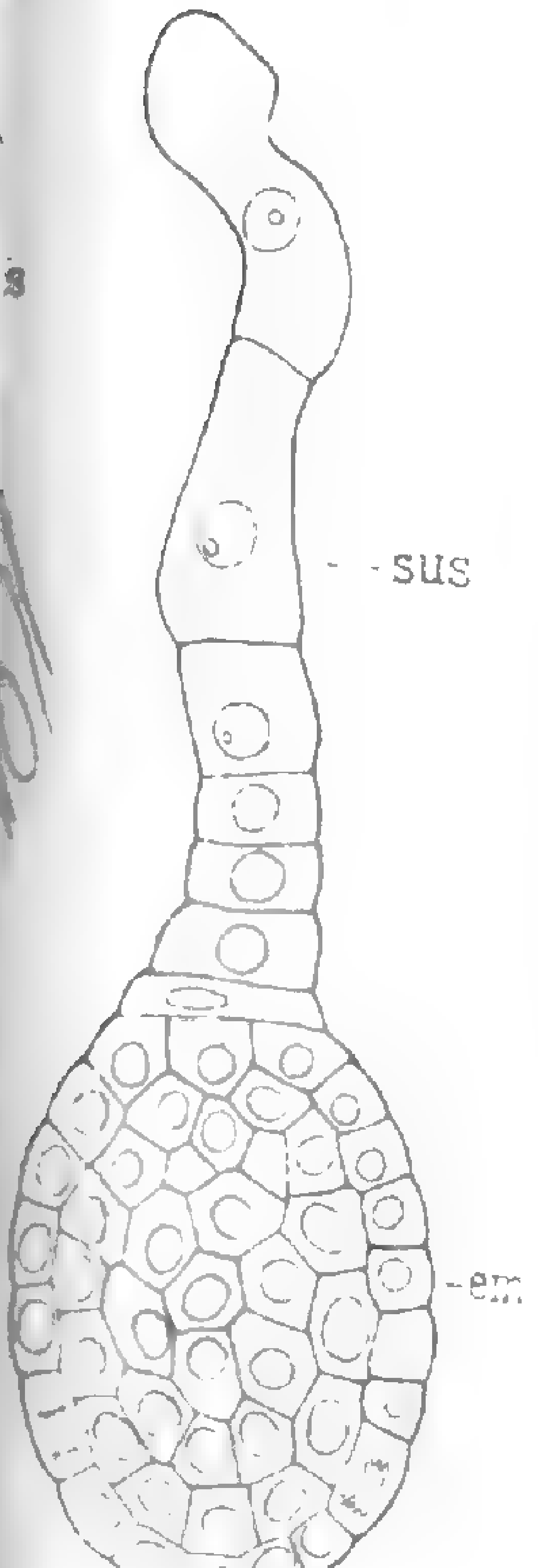

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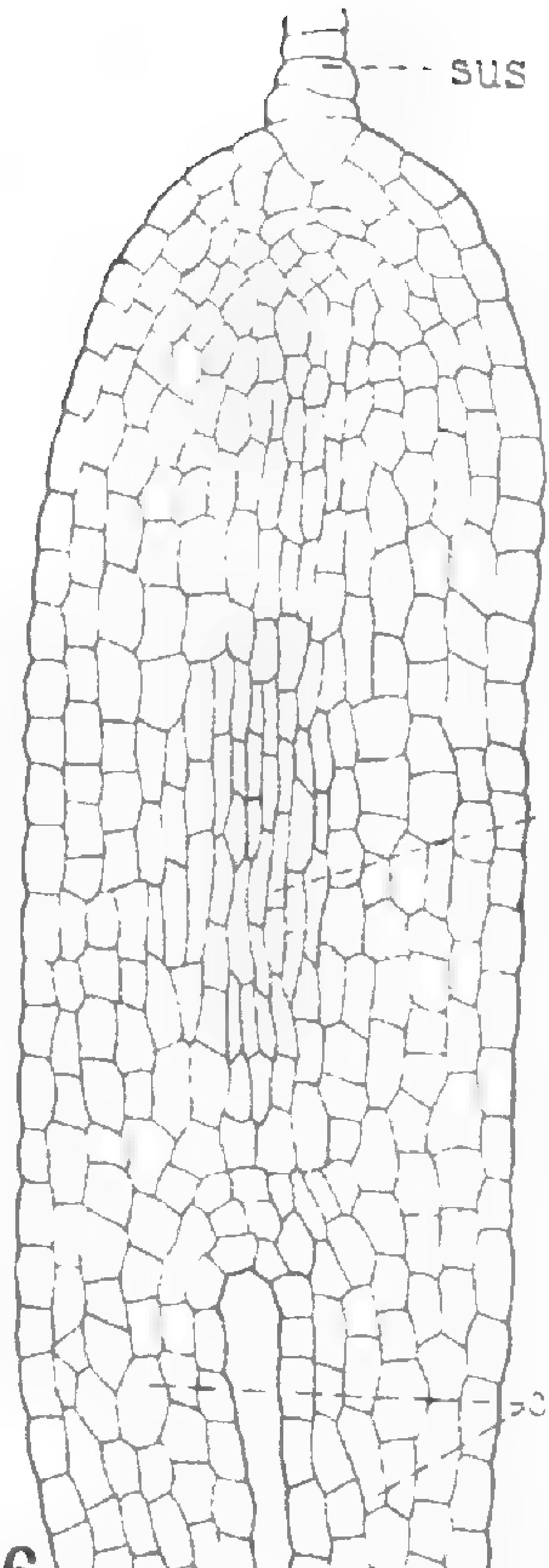

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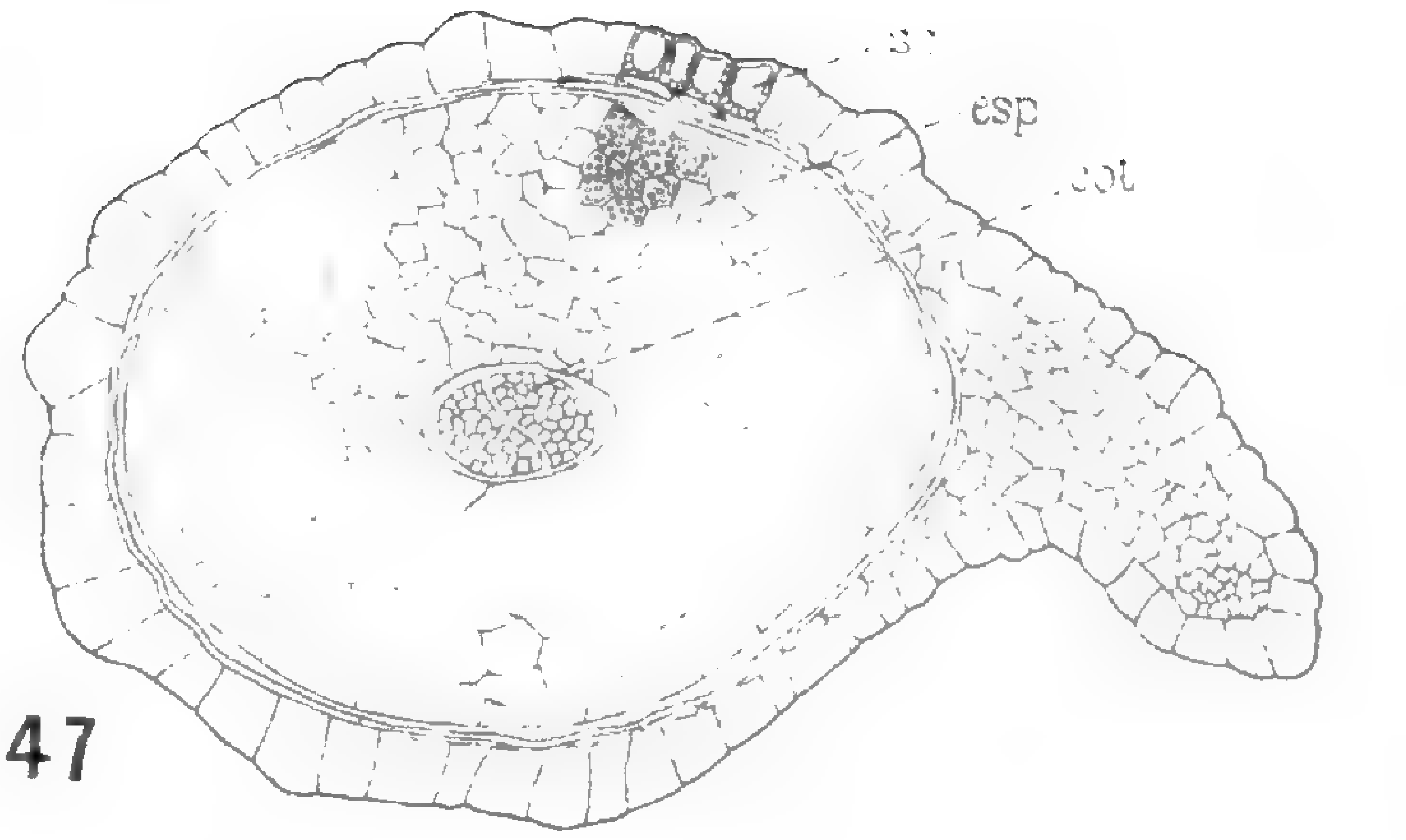

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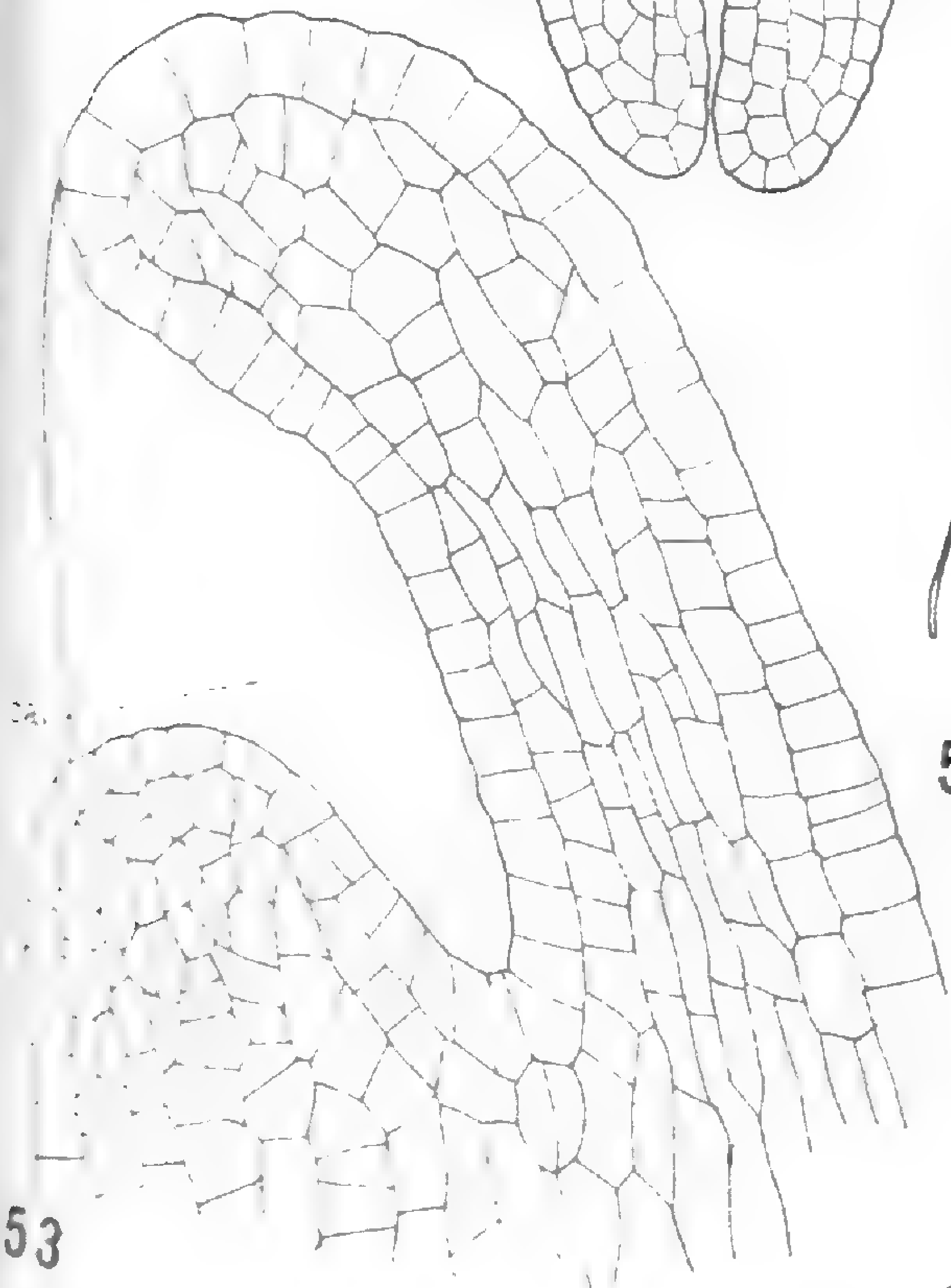

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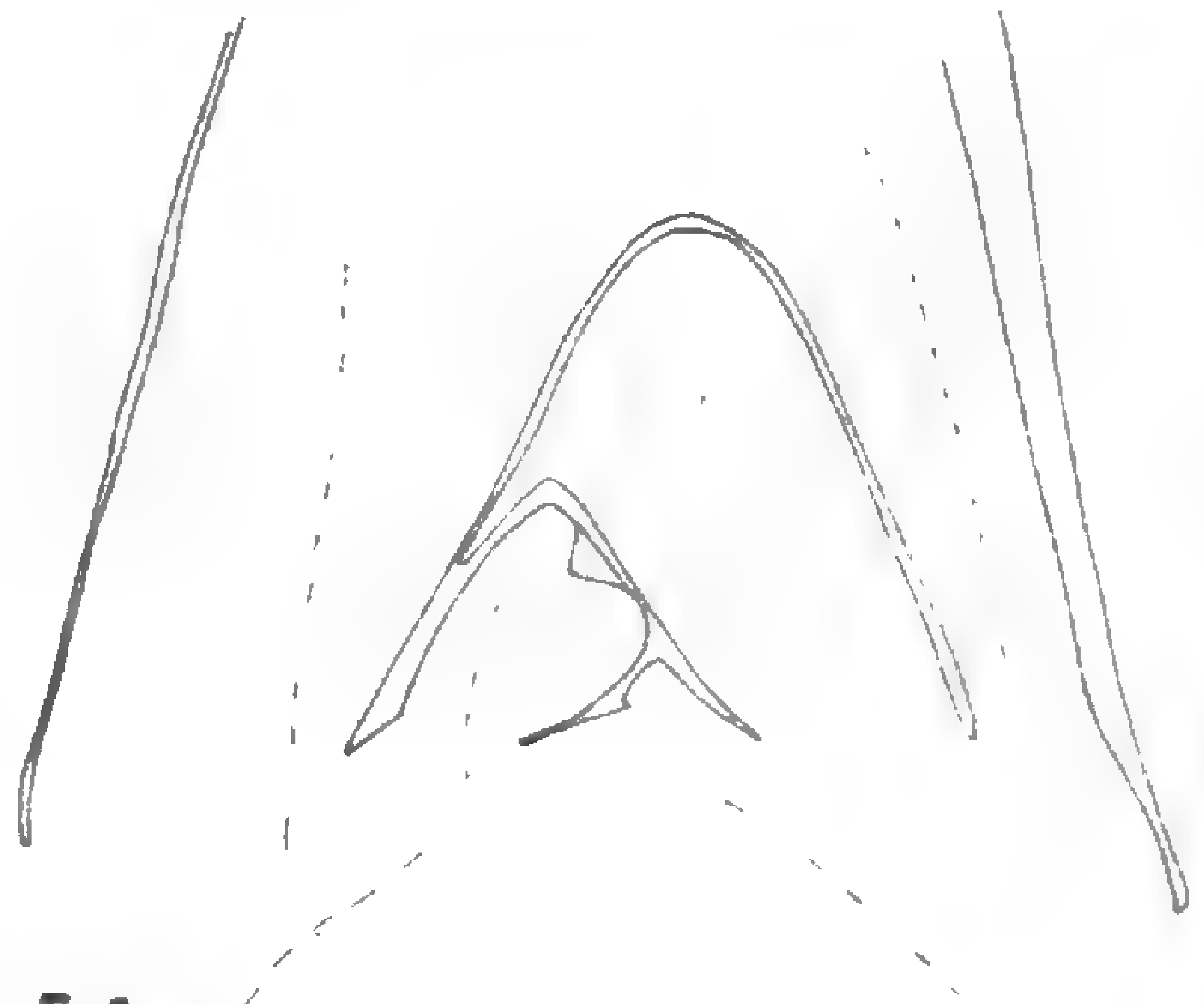

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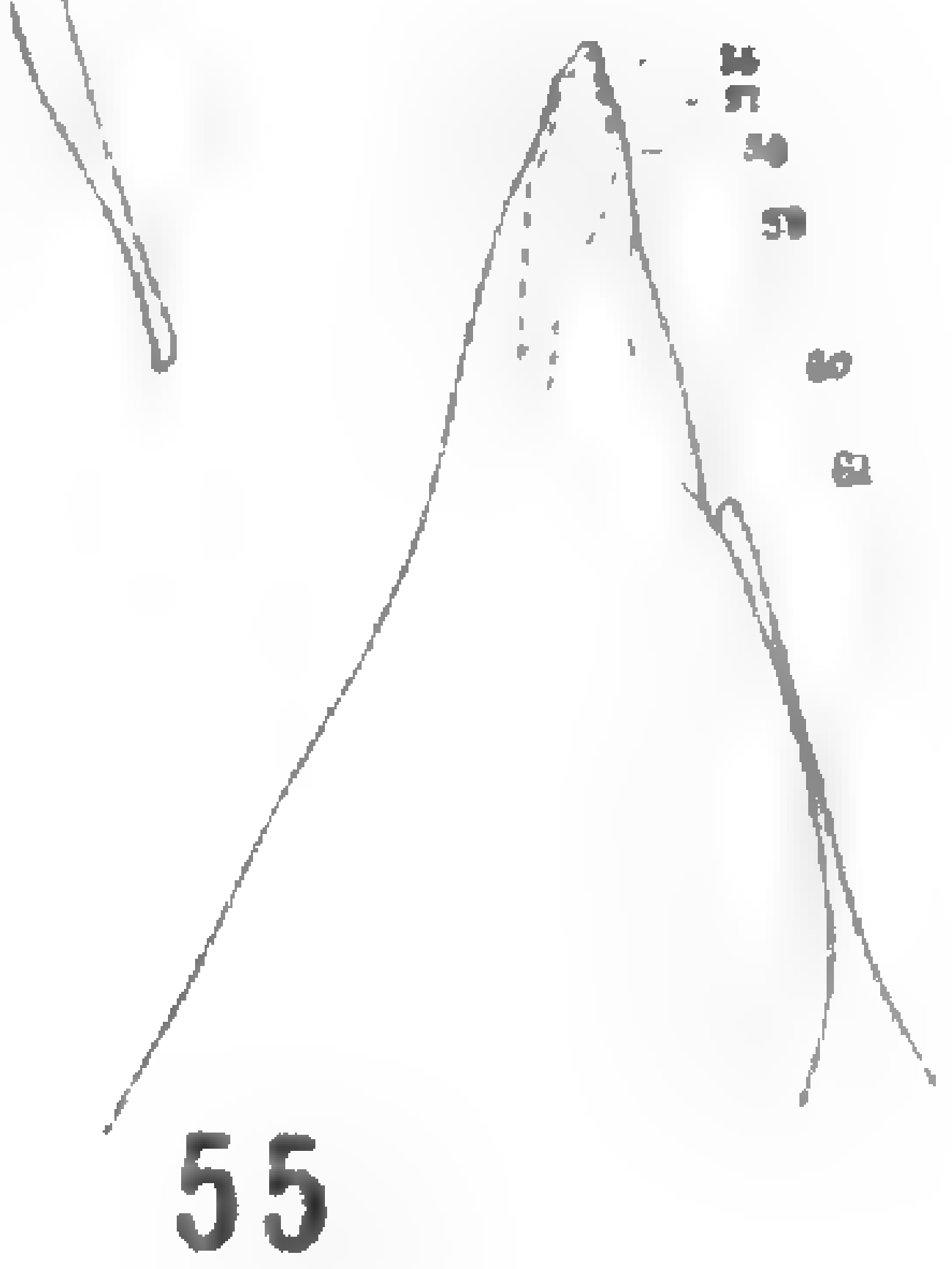

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FIG. 28. Growing point of tip of carpel in umbrella, horizontal section. ×40.

FIG. 29. Stylar umbrella viewed from above; in outline. ×⅔.

FIG. 30. Ovary and style to show the course of pollen tube indicated by dotted line; somewhat diagrammatic. ×2.

FIG. 31. Longitudinal section of stigmatic surface with sprouting pollen grains. ×120.

FIG. 32. Longitudinal section of conducting strand in umbrella of style showing conducting and vascular tissue. ×40.

FIG. 33. Transverse section of upper surface of umbrella of style showing conducting and vascular tissue and glandular epidermis. ×120.

FIG. 34. Transverse section of stalk of style before pollination. ×20.

FIG. 35. Transverse section of stalk of style at time of pollination. ×20.

FIG. 36. Tip of pollen tube from conducting tissue of umbrella; optical section. ×400.

FIG. 37. Cross wall in tube near stigmatic surface. ×400.

PLATE V.

FIG. 38. Longitudinal section of upper end of embryo sac showing fusion of male and female nuclei. ×400.

FIG. 39. Longitudinal section of embryo sac showing two-celled endosperm, columnar tissue, and remains of nucellus. ×120.

FIG. 40. Longitudinal section of embryo sac showing four-celled endosperm. ×120.

FIG. 41. Longitudinal section of portion of ovule showing eight-celled endosperm and integument. ×40.

FIG. 42. Longitudinal section of seed through the wing showing multicellular endosperm and two-celled embryo. ×20.

FIG. 43. Two-celled embryo. ×232.

FIG. 44. Young embryo with suspensor. ×400.

FIG. 45. Older embryo with suspensor. ×232.

FIG. 46. Longitudinal section of embryo from mature seed. ×120.

FIG. 47. Tranverse section of mature seed cutting the embryo through the cotyledons; detail partially filled in. ×40.

FIG. 48. Longitudinal section through the hilum of nearly mature seed. ×120.

FIG. 49. Longitudinal section of germinating seed, with cotyledons; seed coat has been removed; portion beyond the dotted line is that from which aleurone has not yet been removed. ×20.

FIG. 50. Seedling with cotyledons and three epicotyledonary leaves. ×1.5.

FIG. 51. Vertical section through growing-point of seedling. ×232.

FIG. 52. Median vertical section through primordium of first epicotyledonary leaf. ×232.

FIG. 53. Median vertical section through portion of primordium of first epicotyledonary leaf in later stage of development. ×232.

FIG. 54. Vertical section through growing point and young leaves in adult plant. ×20.

FIG. 55. Surface view of primordium of leaf seen from the side, next younger leaf also showing; dotted outline marks cavity of leaf. ×3.

FIG. 56. Transverse section of leaf in *fig. 55* at *56*. ×20.

FIG. 57. Transverse section of leaf in *fig. 55* at *57*. ×20.

FIG. 58. Transverse section of leaf in *fig. 55* at *58*. ×20.

FIG. 59. Transverse section of leaf in *fig. 55* at *59*. ×20.

FIG. 60. Transverse section of leaf in *fig. 55* at *60*. ×20.

FIG. 61. Transverse section of leaf in *fig. 55* at *61*. ×20.

FIG. 62. Later stages of young leaves; cavities shown by dotted outline. ×1

ON THE IMPORTANCE OF PHYSIOLOGICALLY BALANCED SOLUTIONS FOR PLANTS.[1]

I. MARINE PLANTS.

W. J. V. OSTERHOUT.

RINGER demonstrated that animal tissues live longer in a solution of NaCl to which a small amount of KCl and $CaCl_2$ is added than in a solution of NaCl alone. Various explanations of this fact were given by different investigators, all of whom, however, agreed upon the essential point that KCl and $CaCl_2$ are essential for the maintenance of life.

HOWELL assumed that $CaCl_2$ is the stimulus for the heart beat, while NaCl is an indifferent substance, necessary only for the maintenance of osmotic pressure. Similarly RINGER concluded that Ca is the stimulus for the systole, while K is necessary for the diastole of the heart beat.

HERBST made experiments on the influence of the composition of the sea water on sea urchin eggs, eliminating in each successive experiment a different constituent of the sea water. He found that the eggs would not develop in any solution which did not contain all the salts of the sea water. From this he concluded that each of the salts found in sea water is necessary for the development of the egg. LOEB called this view in question as the result of his experiments on Fundulus. He found that this marine fish cannot live in a pure NaCl solution of the same osmotic pressure as the sea water, but that it can live indefinitely in a mixture of NaCl, KCl, and $CaCl_2$, in the same proportions in which these salts are contained in sea water. The fish can also live indefinitely in distilled water. This proves that it does not need any of the three salts mentioned for the maintenance of its life, and that the Ca and K are only required to overcome the poisonous effects which would be produced by the NaCl if it alone were present in the solution (at the above mentioned concentration).

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[1] I wish here to express my sincere thanks to Professor LOEB, who kindly placed the facilities of his laboratory at my disposal and assisted me in every way during these investigations.

It is noteworthy that the Ca and K, which are added to inhibit the toxic effect of NaCl, are themselves poisonous at the concentration at which they are here employed.

These antagonistic effects of Ca and K toward a pure NaCl solution were illustrated still more strikingly in experiments on the egg of Fundulus. The newly fertilized eggs of this fish develop equally well in sea water and in distilled water, but die in a pure $m/2$ NaCl solution without forming an embryo. If, however, a small but definite amount of a salt with a bivalent kation, even of such poisonous salts as $BaCl_2$, $ZnSO_4$, and $Pb(CH_3\text{-}COO)_2$, is added, the eggs will produce embryos. From these and similar observations LOEB was led to formulate his conception of the necessity of physiologically balanced salt solutions, in which are inhibited or counteracted the toxic effects which each constituent would have if it alone were present in the solution.

The blood, the sea water, and to a large extent RINGER'S solution, are such physiologically balanced salt solutions. The observations of HERBST, as well as those of RINGER, are easily explained on this basis. The fact that the elimination of any one constituent from the sea water makes the solution unfit to sustain life does not prove that the eliminated substance is needed by the animal for any purpose other than to counteract the poisonous action of some other constituent of the solution.

Botanists have not thus far made use of these conclusions, for the obvious reason that facts similar to those mentioned above have not been observed in plants. I have recently made a number of experiments which show that there exist in plants phenomena similar to those observed by LOEB on Fundulus and other marine animals.

The species of marine plants chosen for investigation may be divided into two groups:

Group 1 comprises plants which can live a long time in distilled water. It includes the following: BLUE-GREEN ALGAE, Lyngbya aestuarii; GREEN ALGAE, Enteromorpha Hopkirkii; FLOWERING PLANTS, Ruppia maritima.

Group 2 is composed of plants which quickly die in distilled water. It includes the following: GREEN ALGAE, Enteromorpha intestinalis; BROWN ALGAE, Ectocarpus confervoides; RED ALGAE, Ptilota filicina, Pterosiphonia bipinnata, Iridaea laminarioides, Sarcophyllis pygmæa, Nitophyllum multilobum, Porphyra naiadum, Porphyra perforata, Gelidium sp., Gymnogongrus linearis, Gigartina mammillosa.[2]

If plants of either group be placed in a solution of pure sodium chlorid (isotonic with sea water), they die in a short time. This might be attributed to the lack of certain salts which are necessary for their metabolism, rather than to the toxicity of the sodium chlorid. In the case of the plants of Group 1 there can be no doubt on this point, for these plants live a long time in distilled water. If we add pure sodium chlorid to the distilled water it kills them in a very short time. An inspection of the tables will show that these plants in their behavior toward sodium chlorid and other salts, closely agree with those of Group 2, which can live but a short time in distilled water. Sodium chlorid is certainly toxic to the first group, and there can be little doubt that it is so to the second group as well.

The plants of the first group were found in a ditch in a salt marsh through which the tide ebbs and flows; there is always a foot or so of water even at low tide. The salt content of the water fluctuates around a mean of approximately 2.3 per cent.

The plants of the second group were collected at the entrance to San Francisco Bay, where the salt content of the water fluctuates about a mean which is probably not far from 2.7 per cent. The only exceptions are *Enteromorpha intestinalis* and *Ectocarpus confervoides*, which came from wharves in the bay, where the mean salt content is about 2.3 per cent.

All the plants used in the experiments were transferred from the sea water directly to distilled water. After rinsing in this they were placed in glass dishes, each containing 200^{cc} of the solution to be tested. The dishes were then covered with glass plates to exclude dust and check evaporation. Only a small amount of material was placed in each dish. The temperature during the experiments did not vary far from 18° C.

Artificial sea water was prepared[3] according to VAN 'T HOFF'S

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[2] The determinations were kindly made by Professor SETCHELL.

[3] The water used was distilled in glass only and the first part of the distillate rejected. The purity of each salt was carefully tested before using.

formula[4] as follows: 1000^{cc} NaCl, $3m/8$; 78^{cc} $MgCl_2$, $3m/8$; 38^{cc} $MgSO_4$, $3m/8$; 22^{cc} KCl, $3m/8$; 10^{cc} $CaCl_2$, $3m/8$.[5]

This closely approximates the bay water. The plants thrive almost as well in it as in sea water, especially when a very little $NaHCO_3$ or $KHCO_3$ is added to produce a neutral or faintly alkaline reaction.

A series of solutions was tried, beginning with pure NaCl $3m/8$ and adding to it in turn $MgCl_2$, KCl, and $CaCl_2$, either singly or in combination, in the proportions given above. These salts were also used in pure solutions of the same concentration at which they exist in the artificial sea water described above.

It should be said that little difficulty was experienced in determining the death point with sufficient precision. The color reactions and the microscopic appearance of the cells allowed this to be done with sufficient accuracy, so that the results were not in doubt on this account.

The results of the experiments are set forth in the tables. The figures represent the average of four parallel series carried on simultaneously. A control series was also carried on in which each solution was made faintly alkaline by the addition of $NaHCO_3$, $KHCO_3$, or $Ca(OH)_2$. This had a beneficial effect during the first two or three days of the experiment, but the final results were practically the same as in the other series.

From a consideration of the results for Group I we may draw the following conclusions.

1. The plants die much sooner in a pure sodium chlorid solution (isotonic with sea water) than in distilled water. The poisonous effect of the NaCl largely disappears if we add a little $CaCl_2$ (10^{cc} $CaCl_2$ $3m/8$ to 1000^{cc} NaCl $3m/8$); in this mixture the plants live nearly as long is in distilled water. Addition of KCl to this mixture enables them to live longer than in distilled water. Further addition of $MgCl_2$ and $MgSO_4$ enables them to live practically as long as in sea water.

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[4] VAN'T HOFF, J. H., Physical chemistry in the service of the sciences 101. Univ. of Chicago Press, 1903.

[5] This corresponds approximately to the proportion of Ca in the sea water of the bay.

TABLE I.

DURATION OF LIFE IN DAYS.

CULTURE SOLUTION.	GROUP 1			GROUP 2		
	Lyngbya aestuarii	Enteromorpha Hopkirkii	Ruppia maritima	Ptilota filicina	Pterosiphonia bipinnata	Iridæa laminarioides
Sea water (total salts 2.7%)	95	150+	150+	11	24½	24
Artificial sea water: 1000 cc $NaCl$ $3m/8$ 78 " $MgCl_2$ " 38 " $MgSO_4$ " 22 " KCl " 10 " $CaCl_2$ "	90	150+	150+	10½	24½	23
Distilled water.........	30	30	80	1	3½	2½
Tap water.............	32+	36	85	2½	9½	10
$NaCl$ $3m/8$	22	15	23	1¼	3½	4
1000 cc $NaCl$ " 10 " $CaCl_2$ "	29	23	65	2½	6	5
1000 " $NaCl$ " 22 " KCl " 10 " $CaCl_2$ "	35	32	88	3½	10	9
1000 " $NaCl$ " 78 " $MgCl_2$ " 10 " $CaCl_2$ "	29	23	45	3	6	6
1000 " $NaCl$ " 78 " $MgCl_2$ " 22 " KCl "	25	13½	30	2	4	4
1000 " $NaCl$ " 22 " KCl "	23	13½	23	1	2	5
1000 " $NaCl$ " 78 " $MgCl_2$ "	22⅚	13½	25	1½	2	2
1000 " Dist. H_2O 78 " $MgCl_2$ "	15½	16½	19	1	2	2¼
1000 " Dist. H_2O 38 " $MgSO_4$ "	17½	13	23	1	2	2
1000 " Dist. H_2O 22 " KCl "	21	13½	56	1	1⅝	5⅓
1000 " Dist. H_2O 10 " $CaCl_2$ "	26+	12½	58	2½	5	2

TABLE II.

DURATION OF LIFE IN DAYS. GROUP 2.

CULTURE SOLUTION.	Enteromorpha intestinalis	Ectocarpus confervoides	Sarcophyllis pygmaea	Nitophyllum multilobum	Porphyra naiadum	Porphyra perforata	Gelidium sp.	Gymnogongrus linearis	Gigartina mammillosa
Sea water (total salt 2.7 %.)	240	25	11	4½	6	21	33+	11	11
Artificial sea water: 1000 cc NaCl $3m/8$ 78 " $MgCl_2$ " 38 " $MgSO_4$ " 22 " KCl " 10 " $CaCl_2$ "	220	20	7½	4½	6	20	33+	10	9¼
Distilled water	3	1¼	1⅚	2½	2½	3⅓	1⅚	2½	3½
Tap water	10	2¼	3¾	3¾	2½	4½	5½	4½	5¼
NaCl $3m/8$	4¾	⅔	1⅔	⅚	2⅙	3	3	5⅚	2½
1000 cc NaCl " 22 " KCl " 10 " $CaCl_2$ "	68	8	5½	3½	5	14⅙	33+	9	6
1000 " Dist. H_2O 22 " KCl "	4¾	4	1⅚	..	4¾	3	3	4	3

2. The pure solution of each of the salts added to inhibit the poisonous effects of NaCl is itself poisonous at the concentration at which it exists after its addition, since the plants die in such a solution much sooner than in distilled water.[6] A mixture of solutions which are individually poisonous produces a medium in which the plants live indefinitely.

That the plants die so quickly in solutions containing a single salt might be attributed to the fact that the osmotic pressure of some of these solutions is much lower than that of sea water. This supposition is disproved by the fact that in general the plants live longer in tap water than in any solution containing but a single salt, although the tap water has a lower osmotic pressure than that of any solution used in the experiments. (The plants of Group 1 live longer in distilled water also. The tap water is to be regarded as a physi-

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[6] This statement does not apply in all cases to $CaCl_2$, which is the least toxic of the salts employed and for some forms quite harmless in dilute solutions.

ologically balanced solution; this will be more fully discussed in the second portion of the paper.)

3. The poisonous effect of NaCl is inhibited little or not at all by KCl or $MgCl_2$ added singly.

4. The combination $NaCl+KCl+CaCl_2$ is superior to $NaCl+MgCl_2+CaCl_2$, but the latter is better than $NaCl+MgCl_2+KCl$.

5. These effects must be due to the metal ions, since the anion is in nearly all cases the same.

The plants of Group 2 agree with those of Group 1 except in their behavior toward distilled water.

Essentially similar results were obtained from the study of fresh water algae and other plants, the details of which will be given in the second part of this paper.

These results agree in striking fashion with those obtained from the study of marine[7] and freshwater animals[8].

The combination $NaCl+KCl+CaCl_2$ (in the same proportions as in sea water) seems to be quite generally beneficial for animals and plants.

We may in conclusion briefly consider the effects of concentrated solutions. A series of experiments were made on *Enteromorpha Hopkirkii* in which the plants were placed in dishes with a very little sea water. This quickly evaporated, so that the plants became covered with salt crystals in 24 to 48 hours. In this condition some of them remained alive for about 150 days. This means that Enteromorpha plants which remain alive only 15 days in $3m/8$ NaCl solution can live 150 days in an NaCl solution of 10 to 12 times higher concentration, provided the other salts of the sea water are present in the solution (at corresponding concentration) to inhibit the toxic effect of NaCl. Experiments on Lyngbya, Ptilota, and Pterosiphonia gave essentially the same results.

In view of these results, and others of a similar character shortly to be published, it appears certain that physiologically balanced salt solutions have the same fundamental importance for plants as for animals.

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[7] LOEB, Pflüger's Archiv **107**:252. 1905, and the literature there cited.

[8] OSTWALD, Pflüger's Archiv **106**:568. 1905. Univ. of California Publications, Physiology **2**:163. 1905.

RESULTS.

1. Each of the salts of the sea water is poisonous where it alone is present in solution.

2. In a mixture of these salts (in the proper proportions) the toxic effects are mutually counteracted. The mixture so formed is a physiologically balanced solution.

3. Such physiologically balanced solutions have the same fundamental importance for plants as for animals.

THE UNIVERSITY OF CALIFORNIA,
Berkeley.

THE APPRESSORIA OF THE ANTHRACNOSES.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXXXIV.

HEINRICH HASSELBRING.

(WITH SEVEN FIGURES)

IN describing a number of new plant diseases in 1883 FRANK[1] gave an account of peculiar spore-like organs produced by the germ tubes of spores of the bean anthracnose. He showed further that these organs acted as holdfasts, by means of which the fungus was firmly attached to its host during the early phase of development. In the same paper he described analogous organs of *Fusicladium Tremulae* and *Polystigma rubrum*. Almost simultaneously FISCH[2] described the holdfasts of Polystigma, but he did not at all recognize their true significance. He regarded them as "secondary spores" which served in the distribution of the fungus, since the ascospores are embedded in slime when ejected, and are therefore not suited for dissemination by the wind. FRANK first recognized the true nature of these bodies, and gave to all organs of this class the name *appressoria* or adhesion organs. Later MEYER[3] again described and figured the adhesion organs of Polystigma, but added no new observations. In 1886 DE BARY[4] first showed that the complex adhesion organs of Sclerotinia were produced as the result of a mechanical stimulus, but BÜSGEN[5] made the most complete study from a physiological standpoint. He showed that the germ tubes of many parasitic fungi produce adhesion organs of

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[1] FRANK, B., Ueber einige neue und weniger bekannte Pflanzenkrankheiten. Ber. Deutsch, Bot. Gesells. **1**:29–34, 58–63. 1883; Landw. Jahrb. **12**:511–539. *pls. 3.* 1883.

[2] FISCH, C., Beitrage zur Entwickelungsgeschichte einiger Ascomyceten. Bot. Zeit. **40**:851–870. *pls. 2.* 1882.

[3] MEYER, B., Untersuchungen über die Entwickelung einiger parasitischer Pilze bei saprophytischer Ernährung. Landw. Jarhb. **17**:915–945. *pls. 4.* 1888.

[4] DE BARY, A., Ueber einige Sclerotinien und Sclerotinien-krankheiten. Bot. Zeit. **44**:377 et seq. 1886.

[5] BÜSGEN, M., Ueber einige Eigenschaften der Keimlinge parasitischer Pilze. Bot. Zeit. **51**:53. 1893.

various forms, and that their formation is due to a mechanical stimulus resulting from contact of the germ tube with some solid body.

These accounts seem to have escaped entirely the notice of American writers on the bitter rot, as is indicated by the many speculations and by the curious interpretations of the characteristic adhesion organs of the bitter-rot fungus and of other anthracnoses. The first economic account of the bitter rot appears in the *Report* of the chief of the Section of Vegetable Pathology for 1887.[6] Here the formation and germination of the appressoria are described. They are regarded as secondary spores, but no particular function is attributed to them. Excellent figures are also given on *plate 3* of the *Report* of 1890[7]. In 1891 Miss E. A. SOUTHWORTH[8] published the most complete account of the fungus up to that time. Regarding the "secondary spores" Miss SOUTHWORTH says: "What the conditions were that decided their appearance could not be determined. They were produced both in nutritive media and water, but seemed to be especially numerous where the ends of the hyphae came in contact with some hard substance like the cover-glass, and in two cases the addition of an extra drop of nutritive medium had the effect of stopping their formation." As to their function nothing is said, except that they are regarded as resting spores. (See *note*, p. 142.) In 1892 HALSTED published a short account of the secondary spores of anthracnoses.[9] He extends the list of anthracnoses which produce these organs to twenty-five species, including members of both Gloeosporium and Colletotrichum. ALWOOD[10] describes the production of "resting spores" by the bitter-rot fungus, but from his figures and description it is impossible to determine whether he had before him the bodies in question. Other writers have followed these investigators in their interpretation of the peculiar adhesion

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[6] SCRIBNER, F. LAMSON, Bitter rot of apples. Rep. Sect. Vegt. Path. U. S. Dept. Agr. **1887**: 348-350.

GALLOWAY, B. T., Ripe rot of grapes and apples. *Idem*. **1890**: 408

[8] SOUTHWORTH, E. A., Ripe rot of grapes and apples. Journ. Myc. **6**: 164-173. *pl. 1.* 1891.

[9] HALSTED, B. D., The secondary spores in anthracnoses. N. J. Agr. Exp. Sta. Rep. **1892**: 303.

[10] ALWOOD, W. B., Ripe or bitter rot of apples. Agr. Exp. Sta. Va. Bull. 40. 1894.

organs of Gloeosporium. CLINTON[11] regards them as chlamydospores. They are also briefly described by VON SCHRENK and SPAULDING[12] who add *Gloeosporium cactorum* to the list of anthracnoses producing them. In order to clear up the uncertainty expressed in the literature regarding these organs, the following experiments and observations on the appressoria of *Gloeosporium fructigenum* are here recorded.

FORMATION OF APPRESSORIA.

As has been said, DE BARY and BÜSGEN have shown that the stimulus of mechanical contact is the cause of the formation of adhesion organs. Regarding the adhesion organs of Gloeosporium Miss SOUTHWORTH mentions the fact that they are especially numerous where a hypha comes into contact with some hard object like the cover glass. HALSTED finds that a rich nutrient medium produces only a meager supply of "special cells," while pure water increases their production. In neither case were these suggestions further investigated. Other writers had suggested in a general way that "unfavorable conditions" and starvation of mycelium cause the formation of the special cells.

Spores were sown in convex drops of water on slides kept in a moist chamber. Under these conditions the spores germinate rapidly, but their behavior varies according to their position in the drops. Those which sink to the bottom of the drop form a short germ tube, which enlarges into a round or pear-shaped disc when it comes into contact with the glass. In 12 to 18 hours this disc has developed into a complete adhesion organ (*fig. 1*). It is a brown spore-like body, having a thick wall which is perforated on its lower appressed surface with a very distinct germ pore. The adhesion

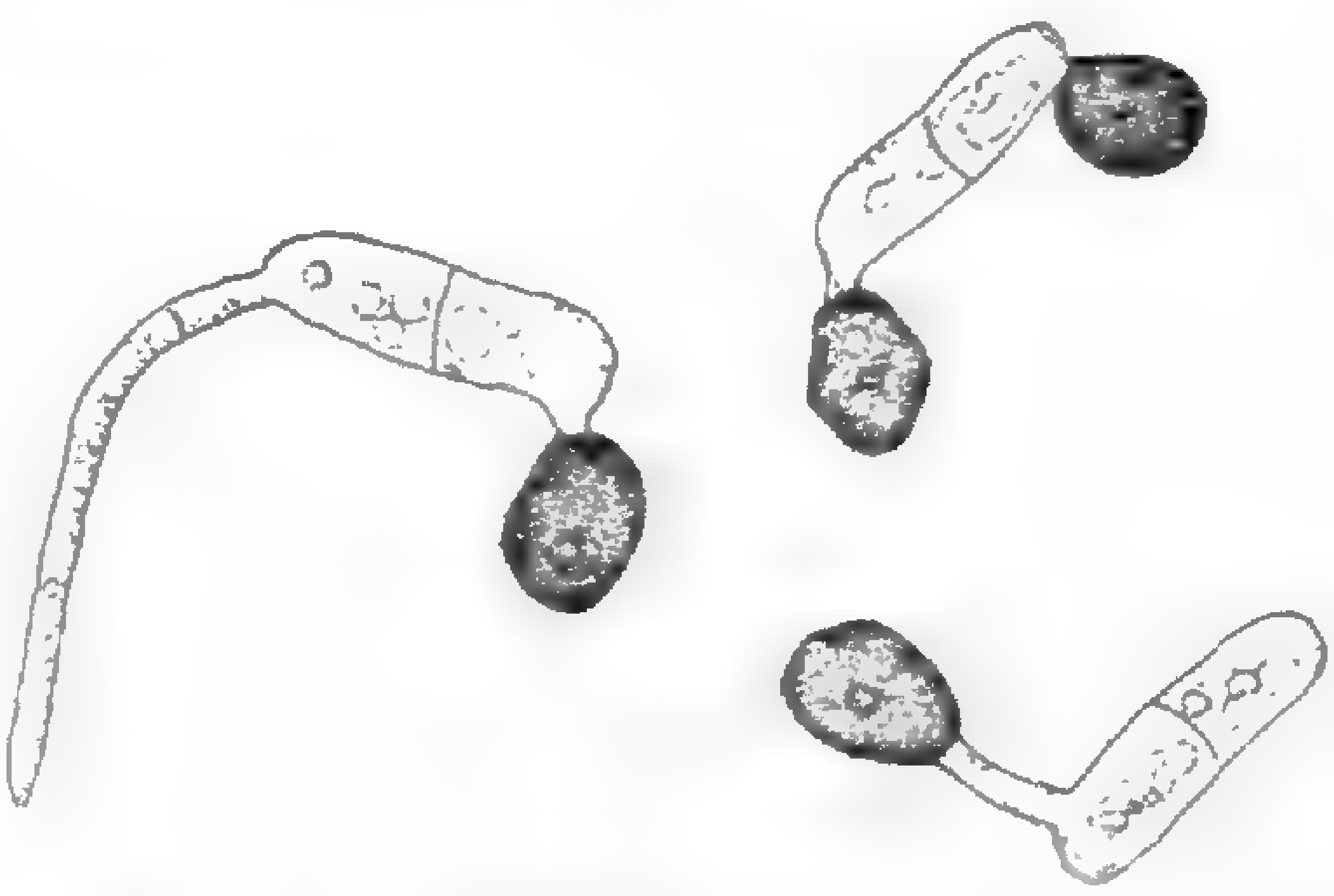

FIG. 1.—Appressoria formed by spores germinating in water on glass slides.

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[11] CLINTON, G. P., Apple rots in Illinois. Univ. of Ill. Agr. Exp. Sta. Bull. 69. *pls. 10.* 1902.

[12] VON SCHRENK and SPAULDING, The bitter rot of apples. U. S. Dept. Agr. Bur. Plant Industry Bull. 44. *pls. 9.* 1903.

organs are so firmly fixed to the slide that they are not easily washed off by a jet of water. Other spores remain floating in the drops of water, being held by the surface film. These also germinate readily, but they never form adhesion discs while the germ tubes remain free in the water. Other spores were sown in drops of water placed on the surface of apples. These behaved in the same way as those on slides. Spores in hanging drops produced mostly mycelia, since very few germ tubes came into contact with the glass. The experiment was then varied by substituting beet infusion for the drops of water. The result was striking. The germ tubes produced no appressoria, but grew out into long hyphae, regardless of the fact that they were often in contact with the surface of the glass or with the cuticle of the apple. When sown in nutrient media of any kind, solid or liquid, the spores of Gloeosporium germinate and form mycelia directly.

These experiments show that the formation of appressoria is induced by a contact stimulus, but in the presence of abundant nutrient material the germ tube loses its power to react to contact stimuli, and the formation of appressoria is inhibited. If this were not the case, the mycelium would react to the contact of every obstacle, such as cell walls or starch grains, which it met in its course through the tissues, and growth would thus be made practically impossible. This is illustrated by the behavior of spores in weak beet infusion. Here the germ tube shows a tendency to form an appressorium, but before this is well formed it grows out again into a mycelial hypha, which immediately repeats the process. In old agar cultures which have been exhausted, the hyphae form a series of thick-walled cells of the nature of appressoria. These do not have the normal shape, but assume fantastically lobed forms, so closely crowded that they resemble sclerotia-like masses. The exhaustion of the nutrient material in the agar and the contact with the glass or other solid particles no doubt leads to the formation of these masses.

GERMINATION OF THE APPRESSORIA.

The appressoria germinate readily on a slide when covered with nutrient solution. The germ tube always emerges from the pore on the surface appressed to the glass. By its vigorous growth it tilts the body to one side (*fig. 2*).

The process of penetration was observed by sowing spores on berries of *Berberis Thunbergii*, which are readily infected by the fungus, although some other species seem to be immune. From the pore on the lower flattened side of the adhesion disc, a slender tube protrudes and dissolves an arrow channel in the wax covering the cuticle. Although at first very slender, the hypha soon becomes larger and dissolves large cavities in the wax (*figs. 3, 4*). The fact that these cavities are more extensive than is necessary for the accommodation of the germ tube would seem to indicate that a solvent is secreted in sufficient quantities to accumulate on the outside of the infecting hypha. Finally the cell wall is perforated and the mycelium branches freely within the cells, at the same time sending hyphae into the neighboring cells. The penetration of the germ tube through the cuticle of the apple has frequently been observed, although it has not been possible to follow the mycelium farther, probably on account of the early collapse of the cells and the consequent accumulation of débris. The channel in this case is very narrow but well defined. Contrary to former supposition no previous injury

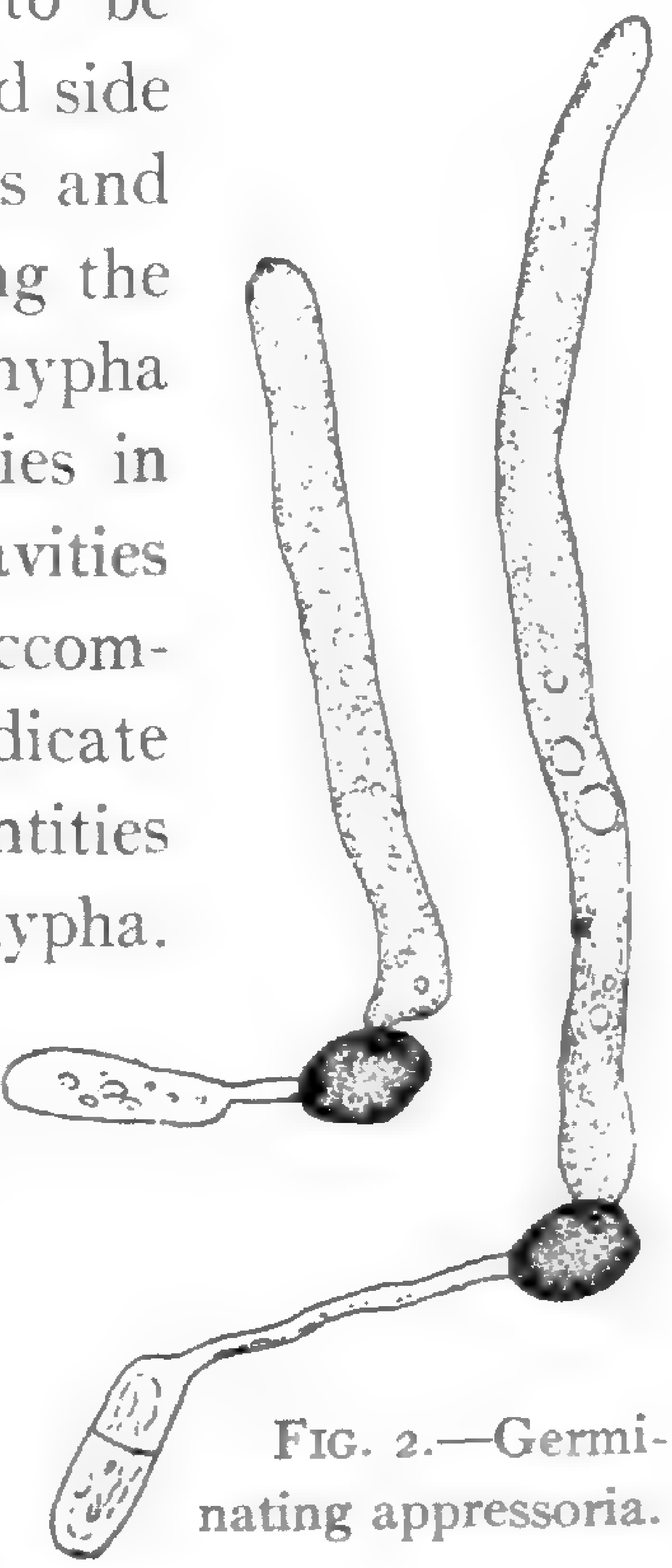

FIG. 2.—Germinating appressoria.

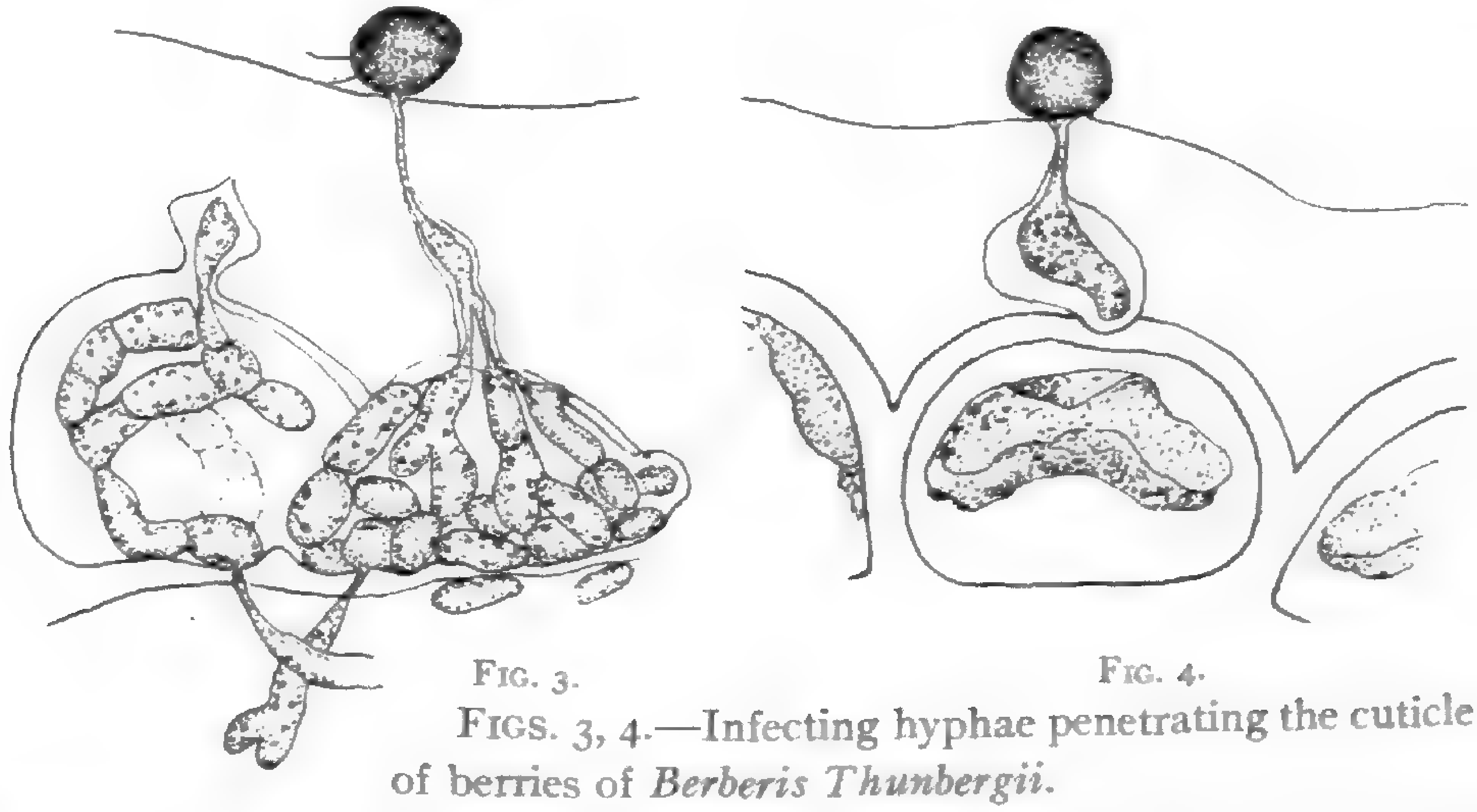

FIG. 3. FIG. 4.

FIGS. 3, 4.—Infecting hyphae penetrating the cuticle of berries of *Berberis Thunbergii*.

or puncture of the fruit is necessary. This is further demonstrated by the number of infections occurring in apples. In some cases 100 to 200 infections were found on single apples, and recently SCOTT[13] reports the enormous number of 1,000 to 1,200 infections on single fruits. It is not likely that these represent previous mechanical injury to the fruits.

APPRESSORIA IN RELATION TO DISSEMINATION.

The behavior of the appressoria of the bitter-rot fungus under natural conditions is of interest from a biological standpoint. The spores of this fungus are imbedded in a gelatinous substance, which causes them to stick together in waxy masses when dry. By reason of this condition the spores cannot be distributed by wind. So far as known they are entirely dependent for their dissemination upon rain, although it is probable that insects take an active part in carrying the spores from tree to tree. Each season the first general infection of apples by the bitter rot is due to rain washing the spores from the limb cankers, in which the fungus hibernates, to the apples below. This is plainly shown by the observation that on a tree the infected apples are distributed within an area that can be circumscribed by a cone having its apex at the canker, the source of infection. Furthermore, drops of rainwater, collected from badly infected trees, usually contain numerous spores of the bitter-rot fungus.

Since the rain, at least in many cases, is the chief factor in distributing the bitter-rot spores, it is of interest to determine the effect of wetting and drying on the spores, and also the relative vitality of the spores and the appressoria. It should be stated, that while the spores are imbedded in their mucilaginous covering, they retain their vitality for a long time, but not during the entire winter, as has often been reported. In the latitude of Southern Illinois, spores remaining on apples under the trees either germinate[14] or perish long before spring. Spores taken from time to time from a diseased apple, which was kept dry in the laboratory from August until January, showed a large percentage of germination as late as Nov. 29, but later rapidly lost their vitality.

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[13] SCOTT, W. M., The control of apple bitter rot. U. S. Dept. Agr. Bur. Pl. Industry Bull. 93. *pls. 8.* 1906.

[14] See also CLINTON, *l. c.*

To test the resistance of spores to drying after being freed from the surrounding mucilage by washing, a quantity of spores was shaken up with water and then spread out on glass slides which were allowed to dry. After remaining dry 14 hours, few spores germinated when again placed in water; after 24 hours, none germinated. At different times during the summer spores were shaken up in water and sprayed on filter paper, apples, and glass slides, but it was impossible to cause them to germinate after having been dried 24–30 hours.

That the appressoria are more resistant is shown by the following experiment. Appressoria were produced by sowing spores in drops of water on slides which were kept in a moist chamber until the following day. The slides were then allowed to dry, all the submerged spores having produced appressoria. The germination of the appressoria was tested from time to time by covering a slide with sugar-beet infusion. The appressoria germinated, though irregularly, as late as Dec. 11, when the last slide was used.

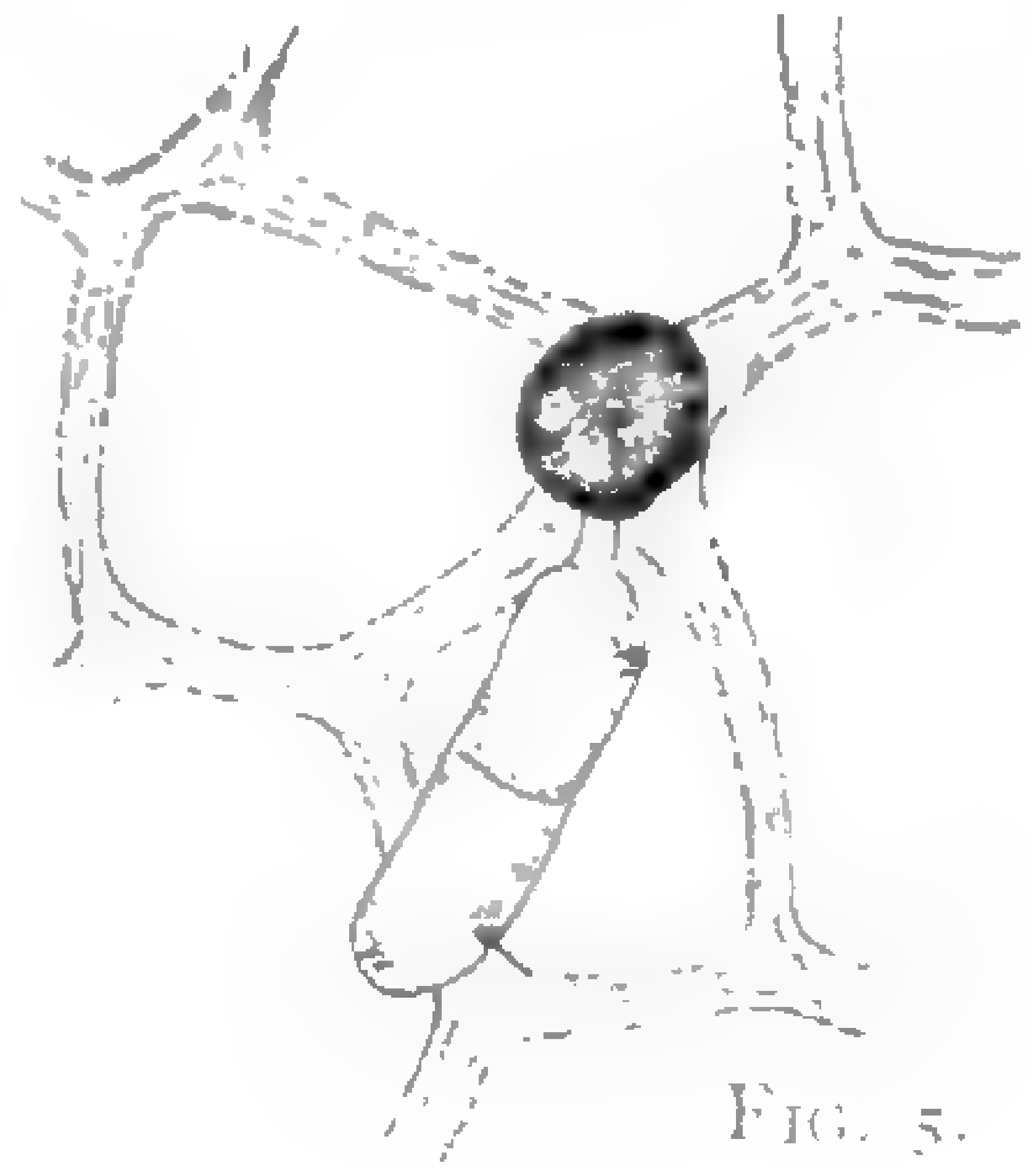
FIG. 5.

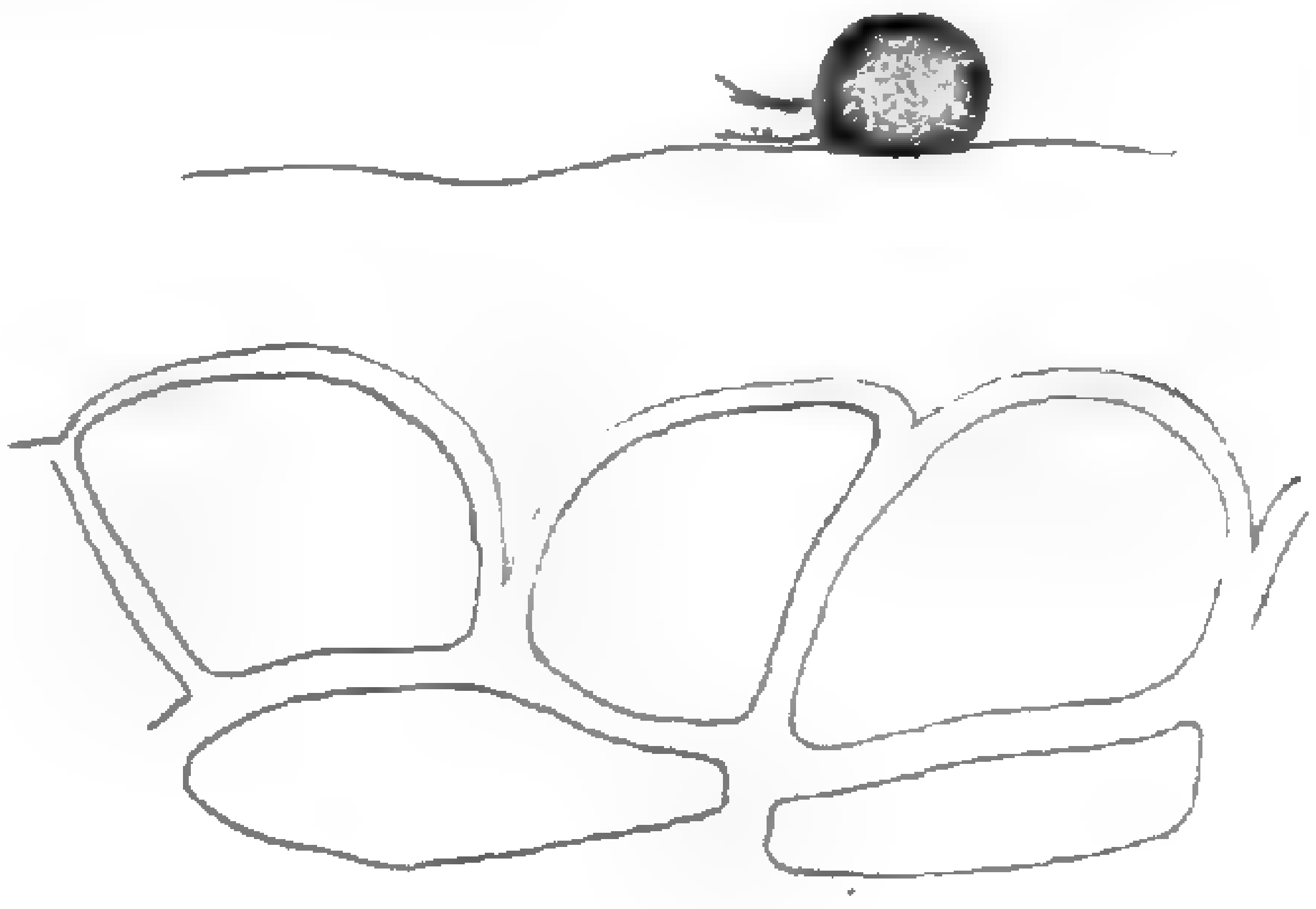
FIG. 7.

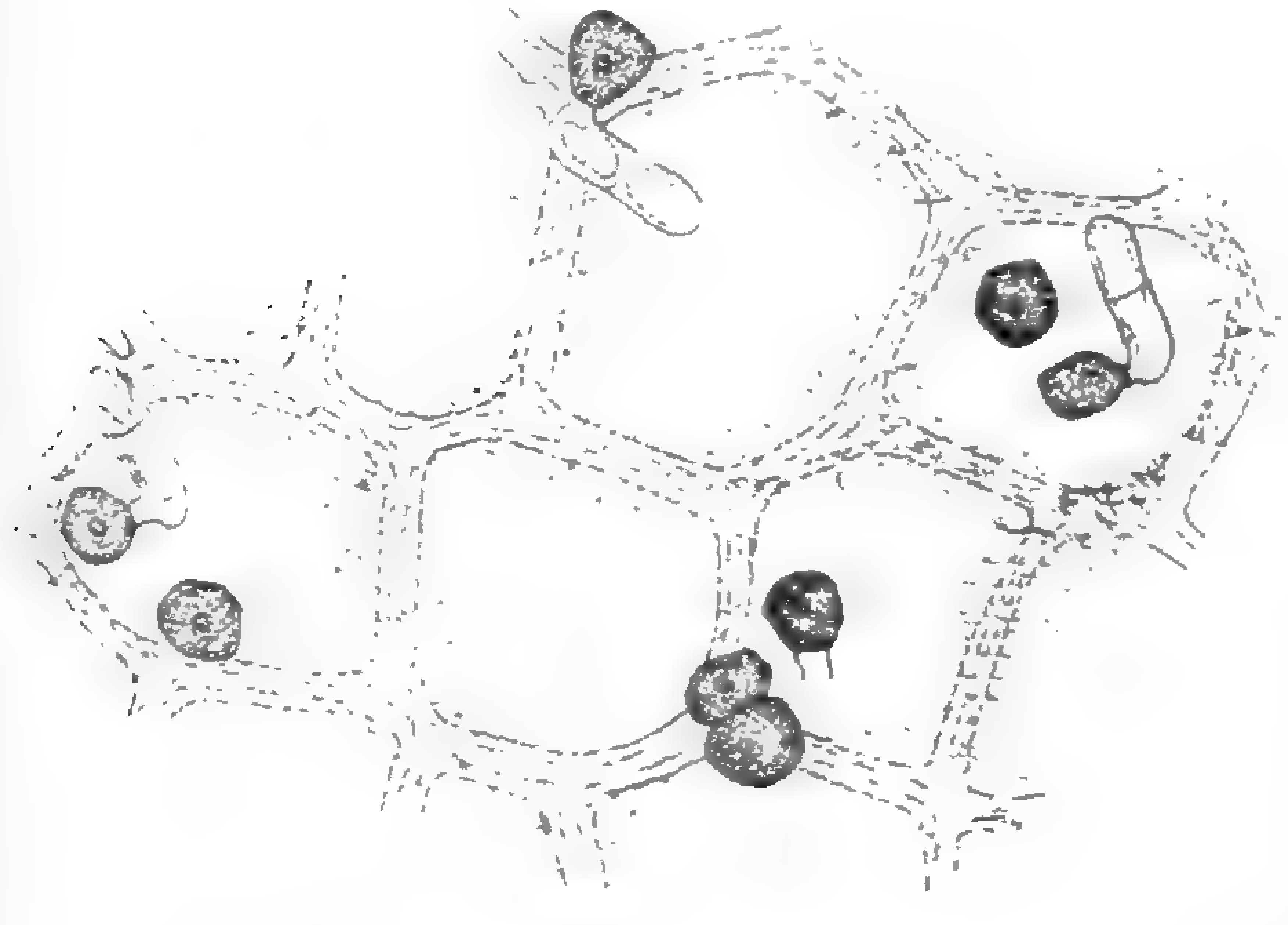
FIG. 6.

FIGS. 5, 6.—Natural appressoria formed on the surface of apples.

FIG. 7.—Section showing relation of adhesion organ to cuticle of apple.

During the hot summer weather the bitter rot spores germinate immediately, and in 12–24 hours the appressoria are formed. Under natural conditions the germ tube is extremely short, since it immediately proceeds to the formation of an adhesion-disc. From this firmly adherent and more resistant organ the infecting hypha dissolves its way into the fruit. In badly infected trees the appressoria can often be found in great numbers adhering to the surface of the apples. Such naturally formed appressoria are shown in *figs. 5, 6*, while in *fig. 7* a single adhesion organ is shown in section.

CONCLUSIONS.

The spore-like organs formed by the germ tubes of the anthracnoses are adhesion organs, by means of which the fungus is attached to the surface of its host during the early stages of infection. They are not suited for dissemination and therefore are not to be regarded as spores. The adhesion discs are formed as a result of stimuli from mechanical contact acting on the germ tubes. When growing in nutrient media the germ tubes lose their power of reacting to contact stimuli by the formation of appressoria. Under natural conditions the appressoria are formed as soon as the germ tube emerges from the spore.

NOTE.—In the same year ATKINSON describes these bodies for a species of Colletotrichum (*C. Gossypii*)[15] and suggests that their production in unfavorable conditions seems to favor the notion that they are resting bodies.

[15] ATKINSON, G. F., Anthracnoses of cotton. Journ. Mycol. **6**:173–8. *pls. 2.* 1891.

THE UNIVERSITY OF CHICAGO.

BRIEFER ARTICLES.

NEREOCYSTIS LUETKEANA.

(WITH ONE FIGURE)

This giant kelp is one of the most common, and certainly one of the most striking algae of the shores of northwest America. Its cylindrical, hollow stalks, as much as 21^{m} long, gradually widening from a diameter of 1^{cm} below to 10^{cm} above, surmounted by a bulb as much as 20^{cm} in diameter and provided with a crown of leaf-like fronds $3–9^{m}$ long; its habitat on submerged rocks over which it forms brown patches acres in extent, a warning to fishermen and pilots, and so dense that only with great difficulty can one get a rowboat through them; its presence everywhere in still waters and stranded along shores, torn loose and transported by waves and wind, attract the attention of every casual traveler along north Pacific shores. Two things concerning this plant at once impress the botanist, viz.: its remarkably rapid growth and its manner of solving the problems of life.

1. *Growth.*—We have here a plant $15–21^{m}$ long,[1] reported to reach a length of over 90^{m},[2] but probably erroneously; MACMILLAN[3] mentions 80 feet. HARVEY[4] states that it is growing at all seasons; fishermen and pilots, however, say that it disappears in winter. I knew the June condition of these plants, and I had accurately located several beds of them near the Marine Station of the University of Washington at Friday Harbor, Wash., during the summers of 1904 and 1905. On March 10, 1906, I made another trip to these beds with a view to determining whether or not this gigantic plant is an annual. The fishermen are partly right. Except for stragglers here and there, the kelps are gone; while those remaining were nearly all decayed and loose, with their fronds mostly torn away. Where the plants were floating freely, the remaining ones were yet in fair condition as to decay, as salt water prevents rapid bacterial action; but it required considerable searching to find a dozen good specimens.

Drifting over the reefs one can see, through a glass-bottomed bucket, on the bottom 3 to 9^{m} below, young plants of Nereocystis 1.25 to 2.5^{m}

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[1] SAUNDERS, Algae of Harriman Alaska Expedition. Proc. Wash. Acad. Sci. **3**:431.

[2] ENGLER & PRANTL, Die natürlichen Pflanzenfamilien 1^{2}:259.

[3] Bull. Torr. Bot. Club **26**:273–299. 1899.

[4] Sea mosses 87.

long, with bulbs 12 to 38^{mm} in diameter, and fronds 30 to 90^{cm} long. It seems that they do not reach the surface the first year, but remain out of reach of waves, pushing rapidly up in the second season only to die when winter overtakes them. A growth of about 18^{m} in the second year, between the middle of March and the first of June, a period of about 70 days, requires on the average a growth of over 25^{cm} a day. The probability is that it is even greater, for March is cool on Puget Sound, so the growth would occur chiefly in the latter part of this period. In proof of this belief is the fact that the ground was frozen during the whole week succeeding the time of observation; in fact, it was the coldest weather of the whole winter. Then too, another trip on May 10, 1906, but to a different bed, revealed none over 6^{m} long; so it is evident that they had 9 to 15^{m} of stretching before them for the next month. Twenty-five centimeters per day is about 0.175^{mm} per minute, which is between one-third and one-fourth as rapid as that reported for the bamboo,[5] and far above that of ordinary plants. One hardly expects prolonged rapid growth in the latitude of Puget Sound, but Nereocystis certainly furnishes an example of it.

FIG. 1.—*Nereocystis Luetkeana.*

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[5] STRASBURGER *et. al.*, A text book of botany, English edition, 231. 1903.

2. *Life relation.*—The shore just below low tide to a depth of 6^{m} is taken up by shorter, broad algae, mostly brown, many green, a few red; limited up shore by the grinding wave-washed rocks as the tide level varies, and by the baking heat of a summer sun during low spring-tides; limited downwards by the decreasing sunlight; we find on this strip the battle ground of the green and brown algae, species against species. Nereocystis, with its tough, flexible, cattle-whip-like stalk 12 to 21^{m} long, rises from the bottom in the deeper waters, a veritable Esau, surrendering to the Jacobs the coveted strip and wresting from the undesired, comparatively unoccupied territory beyond, a highly successful existence. The stalk is firmly anchored to the rocks below by holdfasts covering an area as much as 30^{cm} in diameter. So strong and tough is the stalk, and so firm the attachment, that often a pull of several hundred pounds is necessary to loosen the plant; and then the stalk more often than the holdfast gives way; but a large plant, avoiding quiet waters, needs a firm hold, and one occasionally finds the plants washed ashore with holdfasts dragging rocks as much as 20^{cm} in diameter. The admonition to "build upon a rock" holds for Nereocystis, and the rock must be a big one; those which "build upon sand" are washed away before they reach the adult stage. This is one of the reasons why it grows upon reefs.

Algae love moving water, but few can afford it. Moving water facilitates gas exchange by carrying away that ladened with evolved and lacking in desired gases, and by not depositing suspended materials like quiet water. A layer of beach washings over a plant absorbs sunlight, one of the scarcer commodities of marine algae, any diminution of which only those most favorably located can afford. Nereocystis, by its firm anchorage and long stalks, surmounted by a bunch of tough blades 3 to 9^{m} long but narrow for their length, rides easily in flowing water, and chooses for its home the rocky, clean-swept, tide-washed promontories, where the current keeps its blades horizontal.

Below 6^{m} the brown algae rapidly decrease, and dredging in Puget Sound shows that below 12^{m} they are exceptional. They need light. It is well known too, that the decrease in light downward in water is rapid. This makes the surface the most desirable location. But shore forms, at the surface at high tide, are stranded high and dry at low tide; and those at the surface at low tide are covered at high tide, the depth depending upon the difference between high and low tide. This constant change in water level is one of the greatest difficulties with which seaweeds have to contend. We see at once that marine algae have a very serious problem, to steer clear of the Scylla of darkness on the one hand, and, on the other, at a very short bow-shot's distance, the Charybdis of tide-line destruction by wave and sun. Nereocystis has solved the problem by the floating dock. Its holdfast at the smaller end of the stalk serves as the anchor, fastened far enough off shore to prevent stranding at low tide; its hollow bulb, surmounting the larger, hollow end of the stalk is the float; attached to the bulb are the leaves, constantly at the surface, supple, tough, safe in storm, current, and varying tide. However, it has minor troubles, since in creating for its own fronds an excellent environment it has created also an excellent habitat for other forms as well. It is not uncommon to see the bulbs and stalks densely covered with delicate red and green algae, and hydroids and bryozoa. Rising from unoccupied territory, and creating for its fronds one of the best habitats among marine algae, *Nereocystis Luetkeana* challenges the respect of the botanist and the lover of nature.—THEODORE C. FRYE, *State University, Seattle, Washington.*

TWO NEW SPECIES FROM NORTHWESTERN AMERICA.

MISS EDITH M. FARR of Philadelphia has recently submitted to the writer a small collection of plants for identification. The collection was made in the mountainous regions of Alberta and British Columbia, chiefly in the vicinity of Banff, Lake Louise, Field, etc., during the summers of 1904 and 1905. Among other interesting rarities there are two which the writer has been unable to place satisfactorily in any described species. These are characterized as follows:

Castilleja purpurascens Greenman, n. sp.—Perennial, more or less purplish throughout: stems erect or nearly so, 1 to 3^{dm} high, usually several from a multicipital caudex, glabrous or puberulent below, villous above: leaves sessile, subamplexicaul, linear to narrowly lanceolate, 1.5 to 4.5^{cm} long, 1 to 7^{mm} broad, usually attenuate and acute, entire and undivided or occasionally 3-cleft near the apex, glabrous or the upper somewhat villous-pubescent, 3-nerved; the lowermost leaves much reduced: inflorescence terminating the stem in a subcapitate raceme, later elongating to about 7^{cm} in length, villous-pubescent; bracts ovate-lanceolate to oblong-ovate, 2 to 2.5^{cm} long, usually entire, occasionally cleft: calyx 1.5 to 2.5^{cm} long, and as well as the bracts varying in color from a deep purplish-red to scarlet and rarely to yellow tinged with red or pink, about equally divided before and behind, externally villous with glandular hairs intermixed; the lateral divisions 2-lobed, lobes obtuse: corolla 2 to 3^{cm} long; galea about one-half as long as the corolla-tube, green or greenish-yellow on the glandular puberulent back, with scarlet or magenta colored margins, conspicuously exserted beyond the calyx and floral bracts; lip usually dark green, 3-lobed, about one-fourth the length of the galea, commonly protruding through the anterior fissure of the calyx: mature capsule oblong, 7 to 8^{mm} long, abruptly acuminate or subapiculate, strongly compressed laterally, glabrous: seeds about 1.5^{mm} long, yellowish-brown.

BRITISH COLUMBIA: near Field, at an altitude of about 1200^{m}, 7 June, 1905, Miss *Edith M. Farr*, nos. 567, 568 (type), 569, 570, 571, 572, 573, 574 (form with yellowish inflorescence slightly tinged with red or pink), 575, 576. Type in hb. Field Museum and hb. Univ. of Penn.

The suite of specimens here cited shows considerable variation in color and to some extent variation in foliage, but all have the same habit and technical characters of the flower. The species apparently has its nearest affinity with *Castilleja Elmeri* Fernald, from which it differs in being glabrous or essentially so below, in having a more slender inflorescence, narrower floral bracts, and a more conspicuously exserted corolla with a somewhat longer galea. The purplish cast of the entire plant with the galea extending well beyond the crimson or purplish bracts and calyx renders this an attractive species and easily distinguished among its numerous allies.

Senecio (§AUREI) **Farriae** Greenman, n. sp.—An herbaceous perennial 1 to 1.5^{dm} high: stem erect or ascending, branching from near the base, glabrous except for a persistent white tomentum in the leaf axils; branches few, relatively long and terminated by a single head: basal leaves ovate to slightly obovate, the blade 1 to 3^{cm} long, 1 to 1.5^{cm} broad, rounded at the apex, crenate-serrate to subentire, contracted at the base into a narrowly winged petiole equaling or exceeding the blade, glabrous or nearly so; the lower stem leaves sublyrate or more or less irregularly pinnatifid, the upper reduced to entire bracts: heads about 1^{cm} high, radiate: involucre campanulate, slightly calyculate, tomentulose at the base; bracts of the involucre usually 21, linear-lanceolate, about 8^{mm} long, nearly or quite equaling the flowers of the disk, acute, reddish tipped: ray-flowers 12 to 14; rays orange-yellow; disk-flowers numerous.

ALBERTA: near Banff, altitude 1500^{m}, 8 June, 1904, Miss *Edith M. Farr*. Type in hb. Univ. of Penn., fragment and photograph in hb. Field Museum.—J. M. GREENMAN, *Field Museum of Natural History, Chicago.*

CURRENT LITERATURE.

BOOK REVIEWS.

Plant response.

NO SUBJECT is more fascinating than the responses of plants to stimuli; and though the mechanisms involved are often much simpler than in the case of animals, no subject is more difficult. Papers dealing with limited topics in this field are constantly appearing; one feels some surprise at seeing a large volume of new researches dealing with the matter in the most fundamental fashion. The surprise is increased when it is seen that the author is one whose name is new in the literature of plant physiology and whose nation is fond rather of speculative philosophy than of scientific observation. Professor JAGADIS CHUNDER BOSE of Presidency College, Calcutta, published in 1902 a volume on *Response in the living and non-living*, in which he pointed out many parallels between the "irritability" of organisms and of other bodies. But this volume seems not to have attracted general attention among physiologists; and some of those who read it were inclined to discount the parallelism as one suggested rather by philosophic bias than scientific induction.

On opening this new work[1] the plant physiologist will be inclined to think it some volume on muscle-response in animals, the numerous graphs being quite like those made familiar by the usual records from muscle-nerve apparatus. Closer inspection, however, shows that the author, trained in a laboratory for animal physiology and in the methods of research in vogue for pulse and muscle, has applied these methods to detecting before unsuspected (or at least unrecorded) responses in plants.

But he has done much more than merely apply the existing apparatus and methods. He has employed new methods and has devised new and ingenious apparatus for automatically recording responses. For example, there are described many clever minor adaptations of the optic lever and various electric devices; and among the major ones may be enumerated the kunchangraph (Sanskrit: *kunchan* = contraction) for recording longitudinal contraction in radial organs on applying electric, thermic, or chemic stimuli; the morograph, for recording the death spasm of the contractile protoplasm, and the comparison morograph for recording the response of two plants simultaneously while under different conditions; the shoshungraph (Sanskrit: *shoshun* = suction) for recording the rate of transpiratory suction and its variations; the crescograph,

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[1] BOSE, J. G., Plant response as a means of physiological investigation. 8vo. pp. 781. *figs. 278.* London, New York, and Bombay: Longmans, Green, & Co. 1906.

balanced so as to record the average rate of growth as a straight horizontal line, any fluctuation, even the slightest, showing as deviation from this horizontal line; and the magnetically controlled heliotropic recorder, utilizing the optic lever yet avoiding the use of light within the plant chamber, except that which is the stimulus.

One striking feature of all the apparatus, aside from its ingenuity, is the high magnification which it permits. This is at once an advantage and a danger; but consistent results, if critically controlled, ought to guard against serious error.

The book is not without errors, both of reasoning and fact, into which the author has fallen by reason of some unfamiliarity with his materials. No one could justify himself in accepting as established all the deductions from the vast number of experiments detailed in the book; they must be verified sooner or later by other observers. To our knowledge some have already been repeated (some of those, for instance, on the variation in electric potential resulting from stimulation, in Dr. HARPER'S laboratory at the University of Wisconsin) with concordant results. But whatever the future may show as to the accuracy of details, this book may be acclaimed as a path-breaking one; for it shows a method of attack and a refinement of instrumentation for the study of the phenomena of irritable reactions in plants that are sure to be of the utmost service. It is rather remarkable, indeed, that we have had so few recording instruments in the service of plant physiology, and that we have been content, for example, with magnifications of 10 or 20 times in the auxanometer, where BOSE finds 1,000 or even 10,000 practicable with his crescograph.

The fundamental thesis of the book is that the underlying response to stimuli is alike in plants and animals; is alike in all plants and in all parts, with all stimuli; and is universal. This response, however diverse its modes of expression, consists of two very simple and well-defined factors, contraction and expansion; the former the direct effect of stimulation, the latter the indirect. Mechanical response is always by a concavity of the more excited side and may or may not occur; electrical response can always be detected; growth is merely a multiple response; at death (near 60° C. for phanerogams) a sudden and irreversible molecular change takes place, attended by an excitatory contraction. The phenomena of fatigue, of staircase response when the organ is at first sluggish, of tetanus, of the polar effects of electric currents, of variation in electric potential, of transmission of stimuli, and of rhythmic responses—all can be demonstrated in plants as in animals, giving evidence in greater detail of the essential unity. With this BOSE is more impressed and on it he lays more stress than the case demands; for it is by no means so novel an idea to botanists as to most zoologists.

Of all the fifty chapters in the book none are so unsatisfactory as those on the ascent of sap, constituting part V. BOSE holds that he has demonstrated the ascent of water to be due to the physiological activity of living cells whose suctional response is coordinated by the passage from point to point of an excitatory reaction which drives water in one direction.[2] But some of his reasoning is radically defective, the chapters are full of assumptions, and his experiments are inconclusive. Indeed, he hardly seems to know how difficult a problem he is attacking, and he goes at it with the naïveté of a novice. Such work really tends to prejudice one against the whole book; and caution *is* necessary, for there are other weak spots. In spite of these, the suggestiveness, the ingenuity, and the enormous labor displayed impel us to give this book a most cordial reception. And we shall await with much interest a promised volume on the electrophysiology of plants.—C. R. B.

MINOR NOTICES.

N. Am. Uredineae.—The second part of HOLWAY'S photomicrographs of plant rusts[3] has just appeared, having been delayed several months by a printer's strike. The general character and purpose of this publication were described in this journal[4] upon the appearance of the first part. The present part continues the genus Puccinia through eleven host families, ending with Rosaceae. The photogravure plates carry out fully the promise of the first part.—J. M. C.

Schneider's Handbuch.—The fifth part of the *Illustriertes Handbuch der Laubholzkunde*[5] concludes Drupaceae and includes Pomaceae, and ends the first volume. There are 128 text figures, and a volume index of genera.—J. M. C.

NOTES FOR STUDENTS.

The ascent of water.—After GODLEWSKI'S interesting theory of the relay-pump action of the medullary rays in lifting water seemed to have been completely overthrown by STRASBURGER,[6] who found water still ascending for weeks after treatment calculated to kill living cells, the participation of living cells in lifting water found a champion on theoretical grounds in SCHWENDENER.[7] But PFEFFER[8] hardly dared more than to suggest that they might be of importance in

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[2] See in this connection reviews of other recent papers below.

[3] HOLWAY, E. W. D., North American Uredineae, Vol. I. part II. 4to. pp. 33–56. *pls. 11–23.* Minneapolis, 1906. $2.00.

[4] BOT. GAZETTE **40**:459. 1905.

[5] SCHNEIDER, CAMILLO KARL, Illustriertes Handbuch der Laubholzkunde. Fünfte Lieferung. Jena: Gustav Fischer. 1906. *M* 4.

[6] STRASBURGER, E., Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. Histologische Beiträge **3**. Jena, 1891. Ueber das Saftsteigen. Histologische Beiträge **5**. Jena, 1893.

[7] SCHWENDENER, S., Zur Kritik der neuesten Untersuchungen über das Saftsteigen. Sitzb. Berliner Akad. **44**:911–946. 1892. Gesammelte Unters. **1**:256–297. Weitere Ausführungen über die durch Saugung bewirkte Wasserbewegung in der Jamin'schen Ketten. Sitzb. Berliner Akad. **45**:835–846. 1893. Gesammelte Unters. **1**:298–315. 1898.

[8] PFEFFER, W., Pflanzenphysiologie **1**:203. 1897.

the maintenance of normal conditions in the conducting tissues. Then URSPRUNG rallied to the support of SCHWENDENER with experimental work, and in a paper published two years ago[9] contended that the living cells, either by maintaining the conducting system in condition or by actually lifting, had an important share in the ascent of water. His experiments were carried out on small plants mainly, and he ventured no generalization.

In a more recent paper[10] he reviews critically the direct and incidental experiments of others on this subject, replies to objections raised against his earlier paper; and details further experiments intended to ascertain the precise rôle of living cells. The author adopts a rather hypercritical attitude toward previous results, as is well illustrated by this reasoning regarding girdling: "If at the base girdling 1^{dm} long is borne without injury, it does not signify that this would be the case also at the apex; and if girdling 1^{dm} long does not interrupt the conduction of water, it is not proved that this would not occur with girdling one or two meters long. Hence it follows that the bark (*Rinde*) must be entirely removed if one wishes to form a judgment as to its share in the ascent of sap; and even then one can at most only recognize that it may be dispensed with—not that under ordinary conditions it takes no part in the ascent of sap."

By liberal discounts URSPRUNG arrives at the conclusion that *all* previous researches on this point speak in favor of the participation of living cells in raising water. Even the experiments of STRASBURGER, which have been interpreted as flatly contradictory to such an idea, are counted as offset by his finding that the leaves die after one actually kills 10^{cm} of the stem. For, according to URSPRUNG, the cooperation of living cells throughout the entire length of the plant is necessary; but a small fraction of the conducting system suffices to supply water if in this region the wood cells are living; whereas the whole is inadequate to furnish enough water when they are killed. These living cells do not merely keep the conducting tissues in good condition; they "cooperate in the production of the lifting force," and the component which they furnish is of great significance in comparison with the "purely physical." A notable exception is the beech, in whose older parts the cells of the bark are without influence, "and even in the youngest parts such interaction is insignificant." It is hard to conceive how the living cells in the bark, being outside the water paths, can participate in the work of raising water, and harder still to imagine that they do so in certain plants and not in others.

STEINBRINCK attacks the problem from the "purely physical" side,[11] and

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[9] URSPRUNG, A., Untersuchungen über die Beteiligung lebender Zellen am Saftsteigen. Beihefte Bot. Cent. **18**:145–158. 1904.

[10] ———, Die Beteiligung lebender Zellen am Saftsteigen. Jahrb. Wiss. Bot. **42**:503–544. 1906.

[11] STEINBRINCK, C. Untersuchung über die Kohäsion strömender Flussigkeiten mit Beziehung auf das Saftsteigeproblem der Bäume. Jahrb. Wiss. Bot. **42**:579–625. 1906.

seeks to extend our knowledge of hydrodynamics. He examined the cohesion of water by means of the supersiphon, i. e., a siphon whose legs are so long as to permit the use of columns of liquid too high to be raised by atmospheric pressure, to which (STEINBRINCK thinks erroneously[12]) the action of the common siphon is ascribed. He attempted to ascertain the cohesion of water under various conditions, and met sometimes with such capricious behavior of his apparatus that, more than ever by this experience, he is convinced of the necessity for much more extended physical knowledge before the problem of the ascent of sap can be solved. The reinvestigation of the tension of gases in fern and other sporangia (which he finds nearly at atmospheric pressure) and of their disappearance when the sporangia are wetted, shows that these phenomena do not fall in with any known physical laws; and as these structures plainly contain only dead cells the problem cannot be obscured by dragging in "vital activities" and remains at present inexplicable. How much more caution, then, is needed in the more complex problem of sap movement!

STEINBRINCK finds that a water filament 2^{mm} thick, moving at the rate of 2^{cm} per second, bears a pull of four atmospheres, its tensile strength increasing with diminishing size and rate of flow. Such filaments bear even violent shaking, under certain conditions, without rupture. Their stability is not affected by extremes of temperature that would be encountered in the growing season (say 0° to 35° C.). By ingenious experiments he shows that cohesion may act through membranes, such as the partitions that interrupt the tracheae. As for the objection to the cohesion theory on account of the Jamin-chain condition, he suggests caution on account of deficient physical knowledge, enforcing this by citing the case of gas absorption in the opening sporangia already alluded to. He does not deny the participation of living cells, but can form no conception of the manner in which they act.

EWART, recognizing that water is a liquid of definite viscosity and that the channels through which it moves are small, thereby offering great resistance, has endeavored to ascertain the amount of this resistance in definite cases, and the possible means by which is generated the force necessary to raise water at the required rate.[13] He finds that the flow of water through open vessels is in accord with POISEUILLE'S formula deduced from flow through rigid tubes; hence the velocity is proportional to the pressure and to the square of the radius of the tube, and inversely proportional to the length of tube and viscosity of the liquid. The total resistance in erect stems corresponds to a head of water 6 to 33 (for shrubs and small trees) or 5 to 7 (for large trees) times the height of the plant. Hence, in the tallest trees, the pressure required may be as much as 100 atmospheres. The maximal osmotic suction of leaves in an elm 18^{m} high was 2-3

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[12] STEINBRINCK, C. Ueber dynamische Wirkung innere Spannungsdifferenzen etc. Flora **93**:127–254. 1904.

[13] EWART, A. J., The ascent of water in trees. Phil. Trans. Roy. Soc. London B. **198**:41–85. 1905.

atmospheres, with a total resistance to flow in the trunk of 10–12A. "It appears, therefore," concludes EWART, "that to maintain flow, a pumping action of some kind or other must be exercised in the wood, for which the presence of active living cells is essential. . . . . There is no known means by which these cells can directly pump water in a definite direction. . . . . It is suggested that the wood parenchyma cells, by the excretion and reabsorption of dissolved materials, may bring into play surface tension forces within the vessels of sufficient aggregate intensity to maintain a steady upward flow, and to keep the water of the Jamin's chains in the vessel in a mobile condition, ready to flow to wherever suction is exercised."

But STEINBRINCK declares himself (*l. c.*) unable to form any conception of how such an action can be produced, and LARMOR objects[14] on purely mechanical grounds, saying: "If the osmotic gradient, assisted by capillary pull at the leaf orifices, is insufficient to direct a current of transpiration upward, *capillary* alterations inside the vessels, arising from vitally controlled emission and absorption of material from the walls cannot be invoked to assist." He suggests that *osmotic* changes in the vessels, of peristaltic character, might do; but he apparently does not know that osmotic phenomena do not occur in sap vessels. As a physicist, he inquires whether there is a sufficient stock of energy in the stems for the pumping work required; and he renews the eminently plausible suggestion that the work is done where the external energy is received, viz., in the leaves.

It cannot be said that these researches have solved the problem of water movement. But each in its own way has added something to our knowledge. The more hopeful lines seem to be in determining physical factors and studying more closely the dynamics of the question.—C. R. B.

Gymnosporangium galls.—The anatomical changes induced by *Gymnosporangium clavariaeforme* and *G. juniperinum* on the twigs and leaves of their host, *Juniperus communis*, have been investigated by LAMARLIÈRE[15] with the following main results. The mycelium of *G. clavariaeforme* inhabits the cortex and phloem regions, but does not penetrate into the wood. The cells of the cortex are multiplied and enlarged so that all lacunae are obliterated, resulting in a general hypertrophy of this region. The formation of collenchymatous tissue is almost entirely suppressed. In the phloem region the medullary rays undergo the most marked transformation. Not only do the rays themselves become more numerous, but the cells composing them are also greatly increased in number, so that this tissue is likely to make up about one-half the volume of the bast region. The sieve tubes, parenchyma, and bast fibers retain their normal succession, but owing to the great increase in parenchyma from the rays and from the increased volume of the bast parenchyma, the course of the sieve

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[14] LARMOR, J., Note on the mechanics of the ascent of sap in trees. Proc. Roy. Soc. B. **76**:460–3. 1905.

[15] LAMARLIÈRE, L. GÉNEAU DE, Sur les mycocécidies des Gymnosporangium. Ann. Sc. Nat. Bot. IX. **2**:313–350. *pls. 8–12*. 1905.

tubes and bast fibers becomes distorted and irregular. The cambium ring also is broken and irregular from the fact that uniform differentiation into phloem and xylem no longer occurs. In the wood the medullary rays undergo transformation as in the phloem, becoming irregular masses of parenchymatous storage tissue. The wood is also considerably enlarged.

In *G. juniperinum* the changes are similar but less marked, the greatest changes in the medullary rays being near the periphery. The sieve tubes are mostly suppressed and the xylem is somewhat reduced. In the leaves the chief change induced by this fungus is the transformation of the spongy parenchyma into palisade-like tissue. The observations of this writer agree in detail with the more extensive account of WOERNLE, whose excellent paper on the anatomical changes induced by both the European and American species of Gymnosporangium is nowhere cited or referred to in the article.

As a general result of the effects of the fungus on its host, LAMARLIÈRE points out the tendency toward "parenchymatization," i. e., a tendency of the cells to remain in their more undifferentiated form, a phenomenon from which he draws a parallel to tuber formation.—H. HASSELBRING.

Dioecism among Mucorales.—In continuation of his studies of dioecism among the Mucorales, BLAKESLEE[16] has recently investigated the extent to which differentiation of sex occurs in the spores from germ-sporangia obtained from zygospores. The principal results contained in the paper are as follows. The germ-sporangia of the homothallic species *Sporodinia grandis* and *Mucor* I (undescribed) contain but a single kind of spores, which produce mycelia again capable of forming zygospores. With the heterothallic species the case is different. Here spores in the germ-sporangium may be either all (+) or all (−), or (+) and (−) may be mixed. Of the species tested, *Mucor mucedo* produces all (+) or all (−) spores in its germ-sporangia, showing that a segregation of sex takes place at some period previous to the formation of spores. In *Phycomyces nitens*, however, (+) and (−) spores are mixed in the same germ-sporangium, together with others that show a tendency to produce a homothallic strain. The mycelia of the homothallic strain are characterized by the production of irregular contorted growths to which the writer gives the name *pseudophores*. The production of sporangia on these mycelia is very limited. The spores from them show a segregation into (+) and (−), and others reproducing the homothallic strain.

The reading of this paper is made somewhat difficult partly through lack of clearness in style, which is as essential in scientific exposition as is accuracy in investigation, and partly through the loose use of terms introduced by the author himself. The terms heterothallic and homothallic as used in the earlier papers on zygospore-formation apply to the condition of sexual differentiation of the individuals within a species, strain, or form, being equivalent to dioecious and monoecious. While it is possible to speak of a heterothallic species or race, it

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[16] BLAKESLEE, A. F., Zygospore germinations in the Mucorineae. Annales Mycol. **4**: 1–28. 1906.

is difficult to see how this conception can be applied to individual mycelia or to spores, or even to the process of germination, as is done repeatedly by the author. Perhaps the introduction of new terms is superfluous in this case, for the idea is well expressed by the older terms dioecious and monoecious. These are used in reference to algae, where the condition thus designated exists.—H. HASSELBRING.

Fixation of nitrogen.—The Agricultural Research Association, a Scottish society which has its station at Glasterberry near Aberdeen, has published in its Report for 1905 a paper by the Director of Research, THOMAS JAMIESON,[17] Chev. Fr., F. I. C., which is supposed to overthrow the current knowledge as to the fixation of nitrogen by the root tubercle organisms and to prove that plants of many sorts utilize the nitrogen of the air directly by means of the hairs with which the leaves are furnished. The laudations with which this pretended "research" was received at the annual meeting by men even more ignorant of the subject than the "director of research," are really worthy of a place in comic literature, were it not for its serious side in giving local currency at least to foolish notions.

The "research" itself is its own condemnation, and shows the "director" to be as ignorant of chemistry as of the physiology and anatomy of plants. Here is a serious society in Scotland, spending money for that which is not bread, lauding an imposture as a wonderful discovery, publishing a report with twelve colored plates illustrating the "albumen generators" imagined by a man who does not know the difference between surface hairs and the spiral tracheae of "Holly laurifolia"! Further it summarizes the previous "leading results" of this same "director;" among which we note the discovery that there is "an aperture in root hairs by which the absorption of insoluble matter is explained;" and that the "feathery structures in the flowers of cereals and grasses are not essential parts of the pistil but serve to drive out the anthers to the air"!

Yet we can hardly bring a railing accusation against the misled members of this society when our own postoffice department has had recently to deny the use of the mails, to prevent our own people from being swindled, to a rascal who is advertising "vineless potatoes," that produce a large crop of tubers when planted in wet sawdust and watered with "potatine" at $4.50 per! Truly, some botanical training might save the farmer from his foolish as well as his knavish friends.—C. R. B.

Corky cell-layers in monocotyledons.—MÜLLER describes[18] in detail the cutinized membranes in the root and stem of *Convallaria majalis*, viz., epiblem covering the root-cap, intercutis of greater or less thickness in the cortex of root

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[17] JAMIESON, THOMAS, Report for 1905 to Agricultural Research Association. 8vo. pp. 81. 1905.

[18] MÜLLER, HEINRICH, Ueber die Metacutisierung der Wurzelspitze und über die verkorkten Scheiden in den Aehren der Monocotyledonen. Bot. Zeit. **64**:53–84. *pl. 3.* 1906.

and rhizome, endodermis, and epidermis. The microchemical reactions for each of these layers are given. A process called "metacutinization" is described, which involves all the outer cells of a root-tip, and occurs at the end of the growing season. Four stages in the development of the endodermis are distinguished, following KROEMER, viz., embryonic, primary (characterized by presence of CASPARY'S points), secondary, and tertiary (showing suberization and lignification of a large part of the wall). The endodermis of the root does not usually pass through more than the first two stages. The writer brings together the information available concerning the presence or absence of an endodermis in monocotyledonous stems, and a survey of the tables shows that in about 60 per cent of the species an endodermis is present in the underground stem, while only in Medeola and Scindapsis has an endodermis been reported for the aerial stem. The relation of the starch sheath of aerial stems to the endodermis of rhizomes was also studied, and the writer failed to establish an actual continuity between the two layers. The function of the endodermis is said to be the transfer of water and food between the central cylinder and the cortex, and the increasing cutinization is associated with the necessity for checking the movement of solutes in the radial direction.—M. A. CHRYSLER.

Items of taxonomic interest.—H. D. HOUSE (Muhlenbergia **1**:127–131. 1906) publishes several changes in the nomenclature of Orchidaceae, and describes a new Californian species of Dichondra.—A. A. HELLER (*idem* 134) publishes a new Californian species of Ribes.—Under the editorship of IGN. URBAN (Engler's Bot. Jahrb. **37**:373–462. *pl. 9.* 1906) a fascicle of 18 contributions describing new Andean plants has been published, among which the following new genera appear: *Orchidotypus* (Orchidaceae), by F. KRÄNZLIN; *Laccopetalum* (Ranunculaceae), by E. ULBRICH; *Belonanthus* and *Stangea* (Valerianaceae), by P. GRAEBNER, who gives a general synopsis of the family.—R. PILGER (idem, Beiblatt 85, pp. 58–67) describes a new genus (*Lamprothyrsus*) of South American grasses near Danthonia.—S. LEM. MOORE (Jour. Botany **44**:145–154. 1906) has described 2 new genera from Madagascar: *Cloiselia* (Compositae) and *Stenandriopsis* (Acanthaceae).—R. M. HARPER (Bull. Torr. Bot. Club **33**:229–245. 1906) has described new species from the coastal plain of Georgia under Sporobolus and Nymphaea.—W. H. BLANCHARD (Rhodora **8**:95–98. 1906) has described two new species of Rubus from New England, both of them high blackberries.—A. ZAHLBRUCKNER (Ber. Deutsch. Bot. Gesell. **24**:141–146. *pl. 10.* 1906) has described a new genus (*Lindauopsis*) of parasites in the hymenium of lichens.—R. SCHLECHTER (Bot. Jahrb. **39**:161–274. *figs.* 13–23. 1906), in completing his account of New Caledonian plants, describes the following new genera: *Menepetalum* (Celastraceae), *Acropogon* (Sterculiaceae), *Memecylantus* and *Pachydiscus* (Caprifoliaceae).—J. M. C.

Double fertilization in Carpinus.—In 1893 Miss BENSON published her first paper on the embryology of the Amentiferae. This is now followed by a second paper,[19] dealing especially with the behavior of the pollen tube in connection with double fertilization in *Carpinus Betula*. As the previous paper pointed out, this form is chalazogamic, and usually has several embryo sacs, which develop caeca that penetrate deeply into the chalazal region. The course of the pollen tube varies considerably, but usually it enters the embryo sac at the base of the caecum. Premature arrival of a pollen tube results in more or less branching and coiling about the sacs; and belated pollen tubes also occur, long after fertilization has been accomplished. The polar fusion nucleus is in the caecum, and as the pollen tube passes it one of the male cells (probably the one farthest from the tip) is discharged through a small spur-branch, the other one being discharged upon the arrival of the tip in proximity to the egg. Sometimes the spur-branch, containing a male cell, develops sufficiently to discharge it for the fertilization of the egg of an adjacent embryo sac, in this case triple fusion not occurring. The paper also presents a somewhat elaborate comparison of Carpinus and Casuarina, as the basis of a suggestion that the latter genus should be regarded as a subfamily of Betulaceae.—J. M. C.

Dust spray vs. liquid.—CRANDALL[20] reports the results of a very thorough study of the comparative merits of the dust spray and the ordinary liquid Bordeaux mixture against the scab and sooty blotch of apple and the codling moth and curculio of apple. The dust spray cost about 52 per cent less than the liquid spray and there was further gain in the reduced weight of material to be transported about in the orchard. On the contrary there seemed to be no difference in the thoroughness of application under similar conditions, and the workmen were unanimous in considering the liquid spray the least disagreeable one to apply. And then as to the final and most important test, that of efficiency, CRANDALL says, in conclusion, "The results of the experiments are sufficiently decisive to warrant the conclusion that dust spray is absolutely ineffective as a preventive of injury from prevailing orchard fungi, and that it is considerably less efficient as an insect remedy than is the liquid method of applying arsenites." —E. MEAD WILCOX.

Nature of starch.—In a recent article, FISCHER[21] scouts the idea suggested by CZAPEK[22] that starch may be a mixture of colloidal and crystalline materials, saying that so far as he knows there is not the slightest evidence for such a belief.

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[19] BENSON, MARGARET, SANDAY, ELIZABETH, and BERRIDGE, EMILY, Contributions to the embryology of the Amentiferae. Part II. *Carpinus Betula*. Trans. Linn. Soc. London Bot. II. **7**:37–44. *pl. 6.* 1906.

[20] CRANDALL, C. S., Spraying apples. Relative merits of liquid and dust applications. Bull. Ill. Exp. Stat. 106:205–242. *pl. 1–9. figs. 1–5.* 1906.

[21] FISCHER, HUGO, Ueber die colloidale Natur des Stärkekörner und ihr Verhalten gegen Farbstoffe. Beihefte Bot. Cent. **181**:409–432. 1905.

[22] CZAPEK, F., Biochemie der Pflanzen **1**. Jena 1904.

He does not refer to the work of KRAEMER[23] or of MAQUENNE and ROUX,[24] who independently and from very different standpoints have found evidence of such a mixture. Since starch shows seven characteristic colloidal properties and only two crystalline properties he concludes that it is a colloid.

The author discusses at length the theories of staining with anilin colors, dismisses as wrong the adsorption theory, and concludes that, while in some cases, as in the staining of proteids, the reaction may be largely chemical, in most cases the taking up of the color is by solution, dyes not soluble in water being soluble in starch. He further concludes that the solution is a liquid and not a solid solution, the colloidal starch in the swollen grains being in a liquid state.—EDNA D. DAY.

Heterospory in Sphenophyllum.—This genus has been regarded as strictly homosporous, but THODAY[25] now describes and figures a section through the strobilus of *S. Dawsoni* which shows two adjacent sporangia, one of them containing spores of uniform size, the other containing fewer and larger spores, among which are seen numerous very small aborted ones. These contrasting sporangia certainly suggest heterospory, but the largest of the supposed megaspores has only about 1.5 times the diameter of the spores of the other sporangium. It will be remembered that in *Calamostachys Casheana* the megaspores are only three times as large as the microspores, and this was felt to be a remarkably small difference.—J. M. C.

Proteid metabolism in the ripening barley grain.—The first section of a paper to consist of three has been presented by SCHJERNING.[26] A short notice to call the attention of physiologists is appropriate here, but the reliability of the methods and conclusions must remain unconsidered. The author finds that species, variety, or type *per se* do not affect the chemical composition of the dry matter of the grain so far as the nitrogenous and mineral constituents are concerned. As the grain develops to maturity there is a constant tendency toward equilibrium between the nitrogenous constituents, which is established at maturity and which is not disturbed during subsequent storage except in the case of certain albumins.—RAYMOND H. POND.

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[23] KRAEMER, HENRY, The structure of the starch grain. BOT. GAZETTE. **34**: 341. 1902.

[24] MAQUENNE et ROUX, Sur la constitution, la saccharification et la rétrogradation des empois de fécule. Comptes Rendus Acad. Sci. Paris **140**: 1303–1308. 1905.

[25] THODAY, D., On a suggestion of heterospory in *Sphenophyllum Dawsoni*. New Phytol. **5**: 91–93. *figs. 14.* 1906.

[26] SCHJERNING, H., On the protein substances of barley, in the grain itself and during the brewing processes: First section: On the formation and transformation of protein substances during the growth, ripening, and storage of barley. Compt.-Rend. Lab. Carlsberg **6**: 229–305. 1906.

Lolium-fungus and smut.—In a short paper FREEMAN[27] points out the probability of relationship between the fungus of *Lolium temulentum* and the smuts. Partly by reason of the facts discovered by MADDOX, and later independently discovered by BREFELD and by HECKE, that the loose smut of wheat and the smut of barley can infect the young ovary directly, and that these grains, apparently normal, produce smutted plants, he is led to the belief that the Lolium-fungus is a smut. The behavior and appearance of the smut-mycelium in these embryos is very similar to that of the Lolium-fungus, and strongly suggests a relationship between that fungus and the smuts.—H. HASSELBRING.

Contributions from Gray herbarium.[28]—In the most recent contribution of this series, ROBINSON has published some results of his studies in the Eupatorieae. There is a revision of Piquieria, 19 species being recognized, 4 described as new, and a new sub-genus (*Erythradenia*) established; also a revision of Ophryosporus, 17 species being recognized. Under the genus Helogyne its synonyms are discussed, and its 4 species described (one of them is new). A fourth part of the contribution gives diagnoses and synonymy of Eupatorieae and of certain other Compositae which have been classed with them, among which appear descriptions of 6 new species of Eupatorium.—J. M. C.

N. Am. Characeae.—ROBINSON[29] has published a synopsis of the North American species of Chareae, one of the two subfamilies of Characeae. Of the four genera making up this subfamily, only Chara has been collected in North America. Within the range assigned, 50 species are described as belonging to this genus, 16 of which are characterized as new.—J. M. C.

Assimilation of free nitrogen by fungi.—From a discussion of the results of recent work relating to the assimilation of free nitrogen by fungi, HEINZE[30] comes to the conclusion that elementary nitrogen is not assimilated by fungi other than bacteria The article is useful in that it brings together all the literature relating to this subject.—H. HASSELBRING.

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[27] FREEMAN, E. M., The affinities of the fungus of *Lolium temulentum* L. Annales Mycol. **4**:32–34. 1906.

[28] ROBINSON, B. L., Studies in the Eupatorieae. Contributions from the Gray Herbarium of Harvard University. N. S. No. 32. Proc. Amer. Acad. **42**:1–48. 1906.

[29] ROBINSON, C. B., The Chareae of North America. Bull. N. Y. Bot. Gard. **4**:244–308. 1906.

[30] HEINZE, BERTHOLD, Sind Pilze imstande den elementaren Stickstoff der Luft zu verarbeiten und den Boden an Gesamtstickstoff anzureichern? Annales Mycol. **4**:41–63. 1906.

NEWS.

THE UNIVERSITY OF VERMONT has conferred the degree of doctor of science on Mr. C. G. PRINGLE, keeper of the herbarium of the university.—SCIENCE.

DR. HENRY S. CONARD, professor-elect of biology in Randolph-Macon College, has resigned to accept an appointment as professor of botany in Iowa College, at Grinnell, to succeed Professor FINK.

PROFESSOR R. B. WYLIE, professor of biology in Morningside College, has been appointed assistant professor of botany in the University of Iowa, where he is to have especial charge of the work in plant morphology.

THE APPROPRIATION for the Department of Agriculture for the fiscal year beginning July 1, 1906, aggregates $9,932,940. Among the items of interest to botanists are the following: Bureau of Plant Industry, $1,024,740; Forest Service, $1,017,500; Agricultural Experiment Stations, $974,860; Division of Publications, $248,520; Bureau of Soils, $221,460; Biological Survey, $52,000; Library, $25,880.

FOR TWO YEARS the State Weather Service of Maryland has been carrying on a Botanical Survey of the State under the direction of Dr. FORREST SHREVE, Johns Hopkins University. During the present summer two parties are in the field: one under Dr. SHREVE, working in the Appalachian valley; and one under Mr. FREDERICK H. BLODGETT, Maryland Agricultural College, working in the Blue Ridge region.

THE OFFICE of Experiment Stations of the United States Department of Agriculture has undertaken the preparation of a complete list of the books written by agricultural college and experiment station men in the United States. As a heritage from the Paris and St. Louis expositions the Office has a set of about two hundred books by experiment station men. A list of these and of a few others by the same authors has been prepared, and assistance is requested in completing the list. The Office desires to get copies of such books as are not now in its collection, so far as this is possible.

--THE *Association internationale des botanistes* decided last year at Vienna to form an international organization to advance the interests of agriculture and horticulture by the selection, introduction, and distribution of plants useful for forests, fields, industrial supplies, or ornament. To this end a conference is to be held in Paris, August 25, at the building of the Horticultural Society, 84 rue de Grenelle, where it is expected to organize for this purpose a special section of the Association and to devise means for attaining promptly the ends in view. M. PHILIPPE L. DE VILMORIN is organizing this meeting, which gives promise of being successful, inasmuch as the cooperation of many *savants practiciens* and botanical gardens is already assured.

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Editors: JOHN M. COULTER and CHARLES R. BARNES

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DIFFERENTIATION OF SEX IN THALLUS GAMETOPHYTE AND SPOROPHYTE.[1]

ALBERT FRANCIS BLAKESLEE.

(WITH PLATE VI AND THREE FIGURES)

IN a recent article (**5**) the writer has given a somewhat detailed account of zygospore germinations in certain species of the Mucorineae. The purpose of the present paper is to point out the bearing which the investigations already made in this group may have upon the questions of sexuality in other forms. Some of the problems for research which the facts observed in the mucors would suggest will be indicated, and it is hoped that in forms in which an alternation of generations occurs the distinction between differentiation of sex in the gametophyte and that in the sporophyte will be more clearly drawn than has been done previously. The various grades of differentiation in the gametes themselves or in the gametophyte and sporophyte will not be discussed. The subject for consideration rather will be the sexual condition in the plant as a whole.

According to the sexual character of their thalli, the species of the Mucorineae have been divided (**2–6**) into two main groups, homothallic and heterothallic—designations which correspond in the main to the terms hermaphroditic and dioecious respectively. In a homothallic species the thalli are all sexually equivalent, while in a heterothallic species the thalli are of two different kinds, which have been provisionally designated by the symbols (+) and (−). The sexual character of the (+) and (−) mycelia remains constant when

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[1] This paper was written while working under a grant as research assistant of the Carnegie Institution, to whom the writer wishes to express his indebtedness for the opportunities for research afforded him.

they are grown separately in pure cultures. Thus the opposite strains of *Phycomyces* and *Mucor Mucedo* have been cultivated by means of sporangiospores to respectively 107 and 106 non-sexual generations without apparent change in their sexual behavior. This differentiation into (+) and (−) mycelia, which are capable of retaining their respective characters apparently for an indefinite number of vegetative generations, renders the heterothallic mucors as striking an example of dioecism as is to be found in the plant kingdom.

In those heterothallic species investigated in which a difference in vegetative growth is apparent, the (+) strain is the more luxuriant. In higher forms when a difference in size exists between the two sexes, the female is usually the larger. In such heterothallic forms the zygote develops entirely from the female thallus, and it would not seem unnatural that the thallus which supplies nourishment for the formation of the reproductive bodies should have a greater development than the thallus which produces only the comparatively small male gametes. The zygote of the heterothallic mucors, on the other hand, is formed by the union of morphologically equal gametes cut off from similar branches of the sexually opposite thalli. The zygospore is suspended midway between the (+) and (−) thalli which take equal share in supplying the nutriment for its development. The difference which sometimes exists in vegetative luxuriance between the two strains is independent therefore of the demands of the reproductive bodies, and is to be connected in some way with the primary sexual differentiation into the two opposite strains.

There are no heterothallic species as yet known in which a constant difference between the size of the two gametes has been observed. Two genera from the homothallic group are heterogamic, and in these forms the smaller gamete may be assumed to be male and the larger female. If it were found that a (+) test strain would show a reaction with the male, while the (−) strain showed a reaction with the female branch, one would have evidence for considering the (+) strain female and the (−) strain male. Unfortunately, attempts to hybridize test (+) and (−) heterothallic strains with these heterogamic forms have been as yet entirely unsuccessful. It is to be hoped that other heterogamic forms may be discovered which will lend themselves more readily to experiments in hybridization. That as yet it has not been possible to substitute the terms male and female for (+) and (−), or *vice versa*, does not in the least detract from the conclusion, however, that the differentiation is a sexual one.

Forms characterized by gametes equal in size have been commonly classified as isogamous. The term, it need hardly be pointed out, can have only a morphological application among the mucors. Sexually the two gametes which unite have diametrically opposite characters. The mutual indifference of two mycelia of the same sex, and the active sexual reaction between mycelia of opposite sex which leads to the formation of zygospores when the mycelia are of the same species, and to the formation of imperfect hybrids when they are of two different species, indicate that the isogamy is by no means physiological. The classical researches of BERTHOLD (**1**) have shown that among the morphologically equivalent motile gametes of certain species of Ectocarpus there is a physiological differentiation into gametes which are attractive and those which are attracted, and a similar condition is met with among the Conjugatae. In the mucors the sexes seem to be equally attractive. If in other zygophytic forms the gametes are ever physiologically equivalent, their union can scarcely be considered a sexual process in the usual acceptation of the term.

The physiological differences which exist between the sexually opposite thalli of heterothallic mucors reaches morphological expression in those instances in which the (+) in comparison with the (−) strain is characterized by a greater vegetative luxuriance. Although the heterothallic forms are morphologically all isogamous, the sexual differentiation which they exhibit into two distinct races cannot be considered a lower grade of sexuality than the differentiation shown in the morphologically unequal gametes of the heterogamic species. Heterogamic forms are found only in the homothallic group. It would seem most reasonable to suppose that the isogamous homothallic forms were the more primitive, and had given rise on the one hand to heterogamic forms by a differentiation of the individual gametes, and on the other hand to heterothallic forms by a differentiation of the individual thalli. The partial transformation of the heterothallic species Phycomyces into a homothallic form which has been accomplished might, however, suggest the possibility of a derivation of the homothallic forms from the heterothallic group. There are seven species known to be homothallic, among which three are heterogamic, while sixteen are known to be heterothallic. In all probability the large majority of the species which produce zygospores are heterothallic, yet the sexual character in but a small proportion of the mucors has been definitely determined, and it is unknown whether in this group species may not exist in which sexuality is entirely lacking. The writer has as yet no theories to offer as to the origin of sexuality in the group.

The fact that zygospores when germinating in a proper nutrient medium may give rise directly to a mycelium has led botanists to discard the idea of an alternation of generations comparable to that in higher plants, which was formerly seen in the succession from mycelia bearing sexually formed zygospores to germ tubes producing non-sexual sporangiospores which complete the cycle by the formation again of sexual mycelia. The cytological history of the formation and germination of the zygospores is at present too little known, and the writer would not care to be responsible for advocating as yet a too close homology between the conditions seen in the mucors and in the mosses for example, although the branching out of the germ tube under special conditions to form a mycelium might be considered of no great significance, since paralleled by the capacity of the moss sporophyte to give rise directly to a protonema. The gross analogy, however, between the germination of the zygote in mucors and that in the mosses is much more obvious than between the conditions in the mosses and those in the flowering plants or in animals (**9**), and is sufficiently close to justify one in concluding the mucors in a general comparison of the varying grades of sexual differentiation in the plant kingdom. In the accompanying diagrams and in the ensuing discussion, therefore, the same terminology will be applied to the mycelium and to the germ tube that has been found advisable for the gametophyte and sporophyte of forms in which it is at present orthodox to speak of an alternation of generations.

The terms dioecious, monoecious, and hermaphroditic have been used to designate varying grades of sexual differentiation, and have been applied to both gametophyte and sporophyte. Dioecism among the bryophytes has been understood to signify the existence of two kinds of gametophytes, male and female, and the condition in the sporophyte has been disregarded; while among the flowering plants the usage is changed and dioecism has had reference solely to the sporophyte. An inspection of the accompanying diagrams will show that a plant which is monoecious as regards its sporophyte may be either monoecious or dioecious as regards its gametophyte; and on the other hand a plant dioecious in its gametophyte stage may be either monoecious or dioecious in its sporophyte stage. The first case is illustrated by the ferns, which are all dioecious in the sporophyte though having both conditions in the gametophyte; and the second case is illustrated by the flowering plants, whose sporophytes are either monoecious or dioecious, but whose gametophytes are always dioecious. In flowering plants and in ferns, one of the two generations is characterized by only a single sexual condition, and attention has accordingly been directed to the other generation in which both sexual conditions are present. That this inaccuracy in the terminology has been allowed to stand so long unchallenged is probably due to the tacit assumption that the condition in the ferns is typical for all the archegoniates. Up to the present time, however, the sexual condition in the sporophyte of forms below the ferns has never, so far as the writer is aware, been a subject of investigation or even of discussion.

The terms hermaphroditic, monoecious, and dioecious have established themselves in use, and have their place as technical designations in systematic botany of the flowering plants. As applied to the cryptogams, they have always been unsatisfactory, since the terms hermaphroditic and monoecious are used in descriptive botany to indicate whether the male and female sporophylls are produced in bisexual or unisexual flowers. In the cryptogams the terms lose their distinction with the passing out of use of the word flower. The greater or less local separation of the sexual organs or of the male and female sporophylls on a single individual is of little significance in comparison with the separation of the sexes on two entirely distinct individuals. Whether in Achlya, for example, the antheridia arise from the stalk which bears the oogonium as in *A. racemosa*, or are produced from separate special branches as in *A. prolifera*, is a detail of somewhat minor importance. The sexual differentiation on a single mycelium in the latter species may be perhaps a forerunner of heterothallism, yet in each species the thallus as a whole is bisexual.

Rather than attempt to restrict the terms monoecious and dioecious to either the gametophytic or sporophytic stage, it has seemed best for the purposes of general discussion in the present article to avoid the ambiguity of the expressions now in use by applying a separate set of terms to designate the sexual condition in the gametophyte and sporophyte respectively. Whether or not the precision thereby gained will compensate for the disadvantages of adding new words to an already overburdened vocabulary of technical expressions must rest with botanists whose interest in the subjects of sexuality embraces all the groups of the plant kingdom.

Homothallic and heterothallic are terms already explained, which the writer has used to designate the species of the mucors characterized respectively by thalli sexually all alike, or by thalli sexually of two different kinds. Homothallic and heterothallic forms, therefore, have bisexual and unisexual thalli respectively, and the terms accordingly would correspond to the expressions monoecious and dioecious. Without changing the etymological significance, the meaning of the words homothallic and heterothallic may be appropriately extended to include a description of the degree of sexual differentiation in the prothallus or gametophyte of the archegoniates and spermatophytes, as well as in the thallus of the thallophytes.

Homophytic and *heterophytic* are offered as equivalents in the sporophyte of the terms monoecious and dioecious. Although the "plant" in the common acceptation of the word is the sporophyte in the higher forms, the condition is reversed in the bryophytes. The words homophytic and heterophytic, therefore, as designations for the sporophyte are etymologically not above reproach, but will suffice in lieu of a more cumbersome combination. The terminology suggested has reference to the sexual differentiation as such. The accompanying morphological differences are to be considered as secondary sexual characters and are not included in the classification.

It will now be possible to examine the sexual condition in the


MUCORINEAE
BRYOPHYTES
PTERIDOPHYTES
PHANEROGAMS
SPORODINIA
Homosporangic
Homosporic
Homophytic
Homothallic
PHYSCOMITRIUM
Homosporangic
Homosporic
Homophytic
Homothallic
POLYPODIUM
Homosporangic
Homophytic
Homothallic
PHYCOMYCES
Homosporangic
Heterosporic
Homophytic
Heterothallic
MARCHANTIA
Homosporangic
Heterosporic
Homophytic
Heterothallic
SELAGINELLA
Heterosporangic
Heterosporic
Homophytic
Heterothallic
LILIUM
Heterosporangic
Heterosporic
Homophytic
Heterothallic
MUCOR MUCEDO
Heterosporangic
Heterosporic
Heterophytic
Heterothallic
POPULUS
Heterosporangic
Heterosporic
Heterophytic
Heterothallic
♂
♀
♂+♀

groups represented in the accompanying diagrams. In all the figures the gametophyte has been shaded with parallel lines, the antheridia and zygotes with cross-hatching; while the sporophyte and the sporangia have been left unshaded. The drawings are entirely diagrammatic, and no attempt has been made, therefore, to preserve the relative proportions of the parts figured. As has been already explained, the Mucorineae have been included in this scheme for the purpose of comparison, and the germ tube has been thus homologized with the sporophyte. The mucors then as represented in the first column in the diagram are the only group outlined in which all the three main types of sexual differentiation are as yet known.

In *Sporodinia grandis*, which may be taken as representative of the homothallic group, the mycelium (gametophyte), the germ tube (sporophyte), and the germ sporangia are all alike bisexual. The two opposed gametes, and perhaps the branches from which they are cut off, may not unreasonably be considered unisexual and of opposite sex. It has not been found possible as yet, however, to confirm this assumption experimentally. In the terminology adopted the species is to be considered homothallic, homophytic, homosporic, and homosporangic. The same condition is found in the "monoecious" mosses represented by *Physcomitrium pyriforme*, and in the homosporous ferns represented by Polypodium. The sporangium of the latter is represented as a side branch, since in the ferns, as also in the flowering plants, the sporangia are not simple terminations of unbranched sporophytes of limited growth, as in the bryophytes, but are borne on the sporophylls of a sporophyte more or less highly developed.

If the sexual character of the thallus be preserved, the spores and the sporophyte producing them must be also bisexual. There can be only one type therefore of homothallic forms. Of heterothallic forms, on the contrary, two types are possible—namely, those with bisexual sporophytes, *i. e.*, homophytic, and those with unisexual sporophytes, *i. e.*, heterophytic. These two types are represented by *Phycomyces nitens* and *Mucor Mucedo* respectively.

In the heterothallic species Phycomyces it will be convenient for the purposes of the present paper to neglect those instances in which the germination follows the *Mucor Mucedo* type, as well as the occasional formation of homothallic spores in the germ sporangia, and to consider as typical the condition shown in the diagram. For a more detailed account of the zygospore germination in Phycomyces, as well as for the characters of the homothallic form into which this heterothallic species has been transformed, one must refer to the paper on zygospore germinations already cited. In the type, perhaps somewhat arbitrarily selected for discussion, the germinations are mixed—both male and female spores being produced in a single germ sporangium. The mycelia in this species are unisexual, the zygospores and germ tubes are bisexual, and the spores in the germ sporangia are unisexual. If the germ tube be forced to form a mycelium without the intervention of sporangiospores, a bisexual, *i. e.*, homothallic, mycelium results, which may produce typical homothallic zygospores. Phycomyces as discussed, therefore, is heterothallic, homophytic, heterosporic, and homosporangic.

In the bryophytes, *Marchantia polymorpha* is the only form which has been investigated in regard to the sexual condition of its sporophyte (cf. p. 170). Its gametophyte shows a differentiation into male and female thalli, and the germination of the zygote produces a sporophyte which bears a sporangium containing both male and female spores. Marchantia, therefore, like Phycomyces is heterothallic, homophytic, heterosporic, and homosporangic.

Selaginella, as a representative of the heterosporous ferns, follows in the main the Phycomyces type. It differs from Phycomyces and Marchantia, however, in that it is heterosporangic—the male and female spores being separated in microsporangia and macrosporangia. The spores themselves, moreover, are morphologically of two kinds, the female or macrospores being conspicuously larger than the male or microspores. This morphological differentiation of the spores and sporangia is known only in the heterosporous ferns and in the flowering plants, and is accompanied by a reduction in the size of the gametophyte. Among the homosporous ferns, prothalli are often found with only archegonia or antheridia, and investigators have been able to suppress the formation of one or the other in certain species where archegonia and antheridia occur normally side by side on the same prothallus. The writer is aware, however, of no form among the homosporous ferns which investigators have shown to be strictly heterothallic.

In the monoecious and hermaphroditic phanerogams, illustrated by Lilium, the condition is essentially the same as in Selaginella, with a differentiation into macrospores and microspores, and like the latter species the type may be described as heterothallic, homophytic, heterosporic, and heterosporangic.

The homophytic division of the heterothallic group illustrated by Phycomyces is the only one of the three types that has representatives in all the orders outlined.

Mucor Mucedo represents the heterophytic division of the heterothallic group. In contrast to Phycomyces, the zygospores of this heterothallic species furnish pure germinations, but the spores are unisexual; and while the germ tube and the sporangiospores produced from one zygospore are male, those produced from another may be female. There are, therefore, two different kinds of germ tubes, of sporangiospores, and of sporangia, as well as two different kinds of mycelia. These elements in this species show no more recognizable morphological differences than its mycelia, although the sexual differentiation seems to be as marked as in forms in which such a morphological differentiation exists throughout the whole plant. *Mucor Mucedo* is heterothallic, heterophytic, heterosporic, and heterosporangic.

Since Marchantia is the only heterothallic form among the bryophytes the sexual character of whose sporophyte has been investigated, it is as yet unknown whether any forms of the mosses and liverworts exist corresponding to the *Mucor Mucedo* type.

No heterophytic forms are known at present among the heterothallic pteridophytes, and it will be impossible to say whether they ever existed in geologic times. The non-appearance of one reproductive form on a given sporophyte cannot be taken at once as proof that the species is heterophytic. It not infrequently happens, for example, that one finds only microsporangia on a single individual of Selaginella. Such instances may be compared to the suppression of the organs of one sex on the prothalli of homothallic ferns, and may equally be explained by assuming that the conditions necessary for the formation of the two reproductive bodies do not always coincide.

The "dioecious" phanerogams, represented by the heterophytic form Populus, follow closely the *Mucor Mucedo* type. They differ from *Mucor Mucedo* in that the sexual differentiation has reached a morphological expression, and the sex of the thalli, spores, and sporangia is at once distinguishable. In general the male and female sporophytes are alike in appearance, but in the sporophytes of some forms the sexes are easily distinguished. Perhaps the best known example among the common trees is the Lombardy poplar (*Populus pyramidalis*), which in male specimens has been widely cultivated for the sake of its pyramidal form. The female trees have a spreading habit of growth and are seldom to be found in cultivation.

In the diagram three squares are left blank. In the flowering plants heterothallism has become fixed and no forms of the Sporodinia type exist. There is no reason apparent why heterophytic forms should not occur among the heterothallic pteridophytes. The fact remains that all the existing heterothallic species are homophytic. The blank squares in the phanerogams and pteridophytes must therefore remain unfilled. Little is known about the sexual differentiation in the bryophytes, and it must rest with future research, therefore, to determine whether or not they possess heterophytic representatives in the heterothallic group.

In light of the conditions found in the Mucorineae, the heterothallic bryophytes, as already pointed out by the writer (*l. c.*, p. 25), offer a most interesting field for investigation. Accordingly attention was directed to the heterothallic form *Marchantia polymorpha*, which, according to the unpublished observations of NOLL as reported by SCHULTZE (**17**), retains the unisexual character of the individual thalli when propagated vegetatively by gemmae.

During the last November, Marchantia was found in fruit and sowings were made from individual sporangia, and the young plants resulting from their germination were isolated and transplanted in such a manner that at fructification it would be possible to determine the sex of the individual spores from which they were derived. While the present paper was largely in manuscript, the writer learned of unpublished observations made by NOLL on this same species. Professor NOLL, to whom the writer is greatly indebted for the information communicated, has cultivated Marchantia by means of gemmae for over thirty generations of both male and female strains, without having been able to change the sexual character of the thalli by subjecting them to varying conditions of growth. The form is therefore strictly heterothallic. Moreover, in a single instance a sporangium was made to discharge its spores on a pot of earth, and male and female fructifications were obtained from the mixed growth of thalli resulting from their germination. Marchantia is therefore homophytic, and it now becomes possible to fill out in the diagram one of the two squares which in the bryophytes had been left blank pending the fructification of the young thalli which the writer had obtained from isolated spore germinations.[2]

In Phycomyces, with which Marchantia is to be compared, there seems to be no definite relation between the number of male to female spores formed in a germ sporangium, and it may even happen that all the spores are of the same sex. Moreover, it is not infrequently the case that in a small per cent. of the spores in a germ sporangium the segregation into male and female has not been completed. These bisexual spores produce homothallic mycelia. Cultures from individual spores will be necessary to determine for Marchantia the proportion of male to female spores in a single sporangium, and to ascertain if, in addition to the normally unisexual spores, bisexual spores are ever formed, as is the case in Phycomyces.

The bisexual germ tube of Phycomyces may be cut and forced to branch out to a homothallic mycelium. The observations of Noll and of the writer have shown Marchantia to be homophytic. Its sporophyte as a whole, therefore, must be bisexual, and every cell formed before the determination of the sex of the spores, if brought to develop into a new plant, should theoretically produce homothallic individuals. **Pringsheim** (**16**), **Stahl** (**18**), and **Correns** (**10**), among others, have obtained protonemata from the sporophytes of mosses. No one, however, seems to have succeeded in obtaining regeneration from the sporophyte of liverworts. The writer has experimented with mature sporophytes of Fegatella and with sporophytes of Marchantia of various ages, but has been unable to secure any growth from them.

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[2] While the present paper is in press, 12 thalli have so far produced fructifications out of a total of 113 which were obtained from as many spores from a single sporangium. Of these nine are male and three are female.

In the investigation of the typical germinations of Phycomyces, it has been shown that the determination of sex does not occur in the zygote, but that an interval in the form of a germ tube is interpolated between the zygote and the germ sporangium where the segregation of sex finally occurs. The essential difference between Phycomyces and Marchantia lies in the fact that in the former the interval is a single-celled multinucleate structure arising from a multinucleate zygospore, while in the latter the interval is made up of many uninucleate cells arising from a uninucleate oospore. In Marchantia the segregation of sex undoubtedly takes place at some point in the maturation of the sporangium. If the archesporium and the spore mother cells prove capable of germinating, and it be possible in the thalli which result to recognize the presence of both sexes when the plants are homothallic, one may be in a position to determine the exact point where the segregation of sex occurs and to discover what relation if any the segregation may have to the reduction division or to other nuclear phenomena.

The predominance of organs of a single sex on the prothallus of the ferns due to conditions of growth and the similar phenomenon in the sporophyte of Selaginella may lead to the non-appearance of the other sex. Such a suppression of sex, however, is not to be confused with sex determination. By cultivating fern prothalli under unfavorable conditions of nutriment, PRANTL (**15**) was able to confine the production of sexual organs to antheridia. The archegonia demand a prothallus furnished with meristematic tissue, and consequently on a poorly nourished prothallus which has developed no meristem only antheridia can be formed. If prothalli which are producing exclusively antheridia be removed from a culture medium containing no available nitrogen, to a medium in which available nitrogen is present in sufficient amount, meristematic tissue is developed upon which archegonia are formed. KLEBS (**12**), moreover, has shown that by reducing the amount of light to which they are exposed prothalli may be brought to a prolonged vegetative growth, and thus the formation of both antheridia and archegonia may be suppressed. Professor KLEBS has informed the writer that when the amount of light is increased to a certain extent, antheridia alone are produced from these sterile prothalli, but that to obtain archegonia, they must be exposed to a still greater illumination. BUCHTIEN (7) has shown that in Equisetum external conditions have a similar influence upon the apparent sex of the prothalli.

As yet attempts to influence arbitrarily the sex in unisexual plants have entirely failed. Even though it remain impossible to change the sex in the thalli of Marchantia, it may be found that, by experimenting on the sporophyte where we must assume the sex is unsegregated, one may be in a position to bring about the exclusive production of either male or female spores in a given sporangium. Such a result if accomplished would be analogous to the suppression of one set of sexual organs on the prothalli of ferns.

The behavior of the gametophyte of homothallic ferns and that of the sporophyte of such heterophytic flowering plants as *Melandrium album* (**19**) shows that, abnormally in certain forms and normally in others, only one sex may make its appearance. The conclusion suggested by an assemblage of facts, especially from the animal kingdom, is generally accepted that in so-called unisexual forms one sex is dominant and finds expression in the formation of gametes or spores of the given sex, while the opposite sex exists in a latent condition. However probable such a conclusion may appear for the majority of forms investigated, it must be admitted as at least a possibility that in certain plants or in certain stages a single sex may exist in a pure condition. The fact that besides the occasional production of unisexual germ tubes the zygote of Phycomyces gives rise typically to germ tubes in which the differentiation of sex has not taken place is proof neither for nor against the purity of the male and female thalli, and suggests that the not infrequent occurrence among heterophytic flowering plants of individuals with male and female flowers is as much an indication that both pure and mixed conditions may exist in the sporophyte of these plants as a proof that in heterophytic plants the opposite sex always exists in a latent condition. The germinations of the zygotes of Phycomyces and Marchantia suggest the possibility that the sex may be pure in the gametophyte while mixed in the sporophyte. The observations on unisexual plants, however, have been as yet confined almost entirely to the sporophytic stage, and little is known as to how strict the differentiation of sex actually is in plants in the gametophytic stage.

Unless the gametes contain both sexes, parthenogenesis in homothallic forms should give rise to unisexual individuals—the male gamete to male and the female gamete to female individuals. So far as the writer is aware, no investigations have been undertaken with a view to confirm this assumption experimentally. Attempts made by the writer to determine the sexual character in the gametes of homothallic mucors by means of their germination before or after their transformation to azygospores have not as yet been successful. In the higher plants, parthenogenesis in the sense of the development of an individual from a sperm or egg cell with the reduced number of chromosomes is, so far as the writer is aware, not definitely known to occur. The sex in the apogamous seeds of Taraxacum for example, however, must contain male characters if the plants produced from them develop stamens, as seems regularly to be the case.

What the essential difference between sex actually is, is as yet beyond conjecture, and the significance of sex in organic development is at present a subject of conflicting discussion. It is to be hoped that a further study, especially of lower forms, where the gametes are more closely connected with the vegetative portions and the zygotes formed by their union more accessible to manipulation, may lead to a better understanding of some of the fundamental problems of sexuality. The present brief article is no place for any detailed discussion of sexuality in the various groups of plants. For a short general presentation of the subject, the reader may refer to the recent work of KÜSTER (**13**) and to the literature therein cited. It seems not out of place, however, to say a few words in regard to the thallic differentiation in the lower cryptogams, where the subject has received little attention.

Unisexual and bisexual forms occur throughout the plant kingdom, and are often to be found in the same genera. This sexual differentiation seems to have no relation to the stage of phylogenetic development. Thus while in higher animals the unisexual condition predominates, in higher plants the monoecious, *i. e.* homophytic, condition is the more common. Again, the majority of the ferns are homothallic, while the majority of the mucors investigated are heterothallic. Both conditions, therefore, may be expected *a priori* in any group under investigation, whatever may be its phylogenetic rank.

In groups in which sexuality is present, in both fungi and algae, there are many forms for which the sexual spores have been but rarely found or are entirely unknown. The absence of sexual reproduction may be due (1) to constitutional sterility, (2) to conditions of growth unfavorable to the production of sexual organs, or (3) to the fact that the form is heterothallic and thalli of both sexes have not been found together. In the last case the apparent sterility would not be due to a lack but rather to an excess of sexuality which separates the male and female individuals. Even in heterothallic species, neutral races have been found to exist, and the conditions within which sexual reproduction is possible are frequently very limited.

A morphological investigation may suffice to show that the male and female organs are borne on the same thallus, and the form in question can then be at once classified as homothallic. A heterothallic condition, on the other hand, can never be recognized by a morphological investigation alone. The appearance of but one set of sexual organs on an individual form studied under the microscope may be due either to dichogamy or to suppression of the other sex brought about by conditions of growth, as well as to a unisexual character of the thalli. Carefully conducted cultures are therefore essential to a determination of the sexual character of forms investigated. A few examples may be briefly given to illustrate the necessity of employing the cultural method in a study of even well-known forms. Many other examples equally as appropriate will suggest themselves to the reader.

In the mosses the leafy shoots arise from an inconspicuous protonema, and if certain shoots bear only antheridia and others only archegonia, a cursory investigation would lead one to consider the forms heterothallic, especially if the antheridial and archegonial "plants" differ in appearance. *Funaria hygrometrica*, for example, is classified as monoecious by LIMPRICHT (**14**) and CORRENS (**10**), yet CAMPBELL (**8**, p. 187) says "Funaria is strictly dioecious." The term here is perhaps used in reference to the constant separation of the sexual organs on different shoots without regard to their ultimate connection on the protonema; yet the latter is as an essential part of the plant as the leafy axis, and if the species is in fact homothallic it is not to be called dioecious. Such forms as Funaria offer an interesting field for regeneration experiments to determine if protonemata developed from antheridial and archegonial shoots differ at all in sexual character.

Among the algae, Spirogyra, to mention a simple example, is a familiar genus in which homothallic species are known to occur, and in which heterothallism is strongly to be suspected for certain species from a mere morphological investigation. In *fig. 1*, which is taken from STRASBURGER'S textbook, is represented *Spirogyra longata.* It seems in this type to be a matter of indifference whether the two conjugating cells come from the same or from different threads. Obviously here the filaments are bisexual and the species is therefore homothallic. In Debarya, represented in *fig. 2*, the zygospores are formed, as in the heterothallic mucors, midway between the two thalli, between which no differences are apparent. In the most common form of conjugation, however, which is represented in *fig. 3*, one filament seems to be receptive, since it contains all the zygotes formed between two conjugating filaments and has therefore been considered female. Though rather improbable, it is yet imaginable that a filament which acts as female toward one thread might function as male toward another. Theoretically it would not be a difficult task to determine by cultivation the sexual character of any form found producing zygospores.

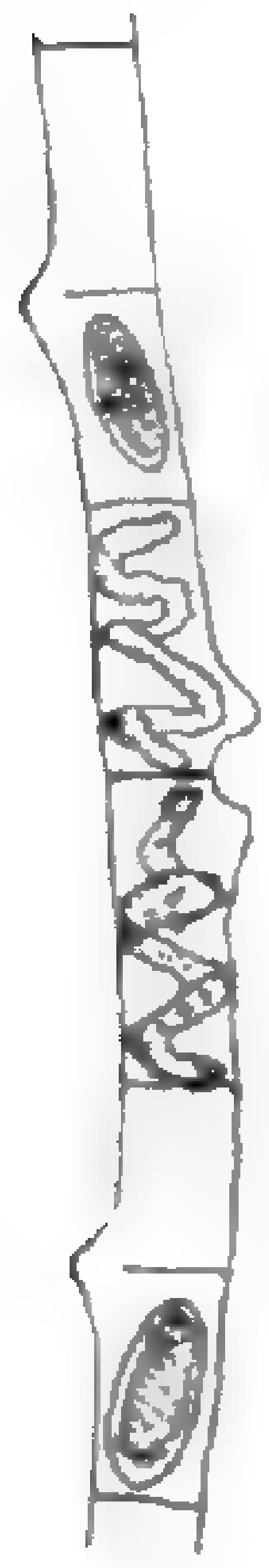

FIG. 1
Spirogyra

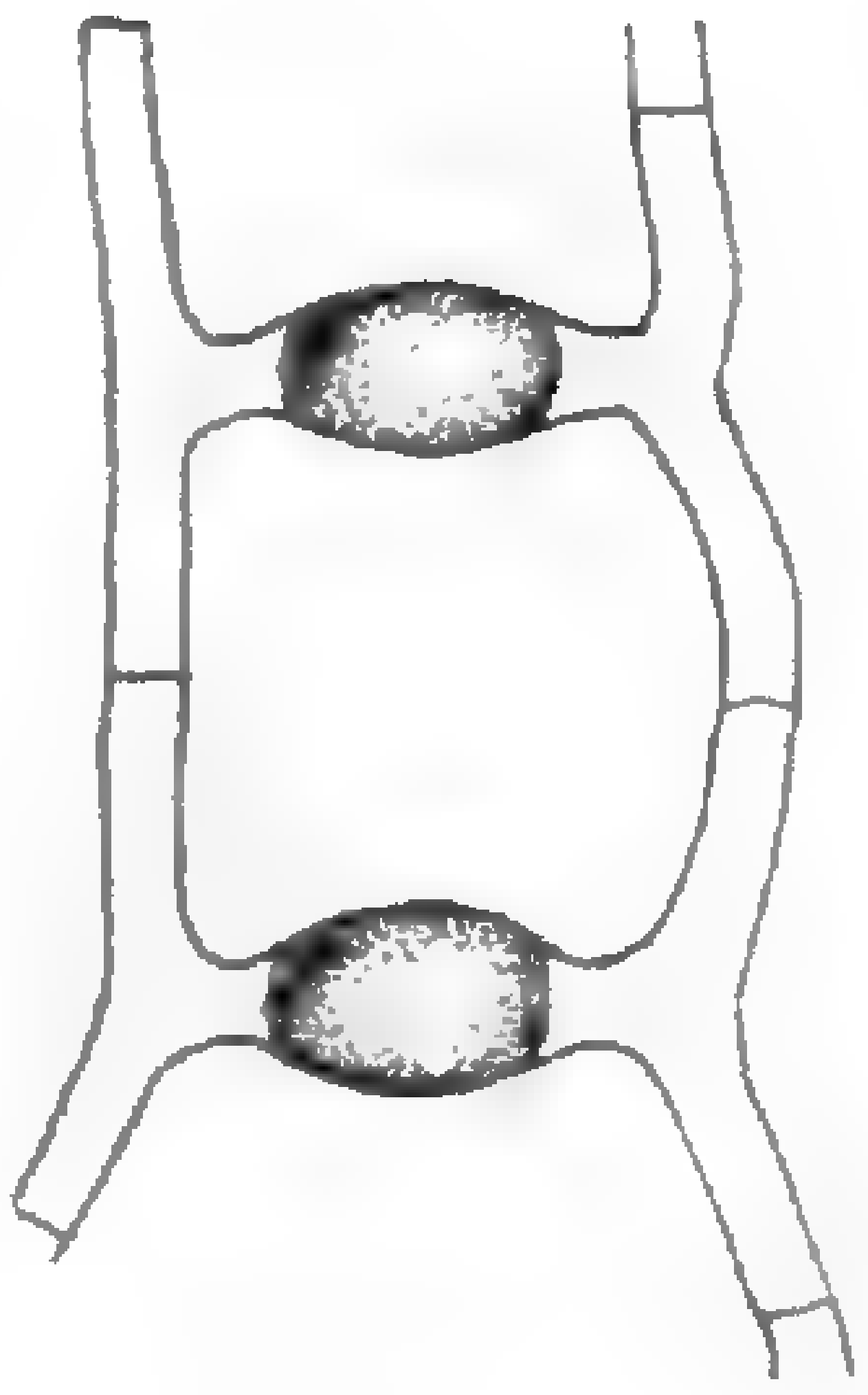

FIG. 2
Debarya

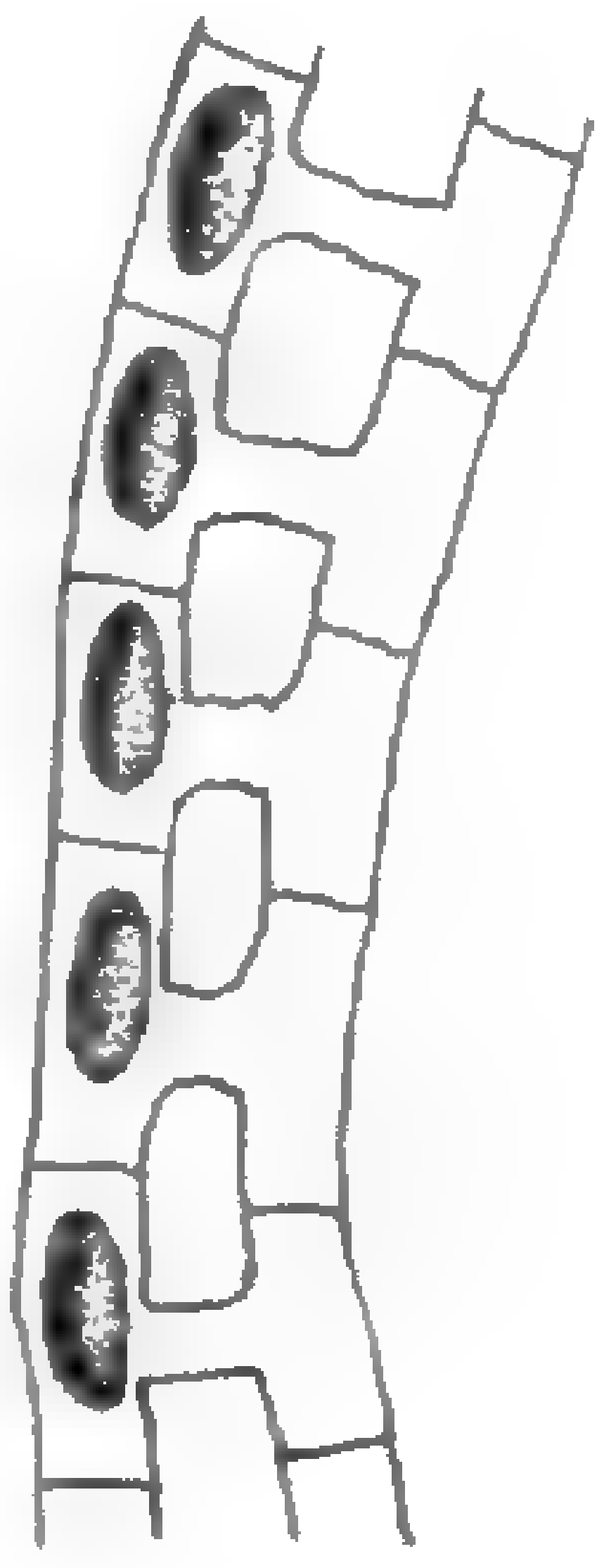

FIG. 3
Spirogyra

The Saprolegniaceae form sexually one of the most interesting groups among the fungi. In *Achlya racemosa* the antheridial branches are borne from the stalk of the oogonium, in *A. polyandra* they arise fom differentiated branches which are only distantly connected with the hyphae which bear the oogonia, and in *Saprolegnia dioica* and *S. anisospora* we have forms which have been described as dioecious. Cultural investigation alone can determine whether these latter forms are in fact heterothallic. It is perhaps significant that in this group forms have been found which have remained sterile under cultivation (*cf.* HORN, **11.** p. 232). It is not improbable that they may represent unmated strains of heterothallic species.

Of especial interest will be an investigation for the possible occurrence of two sexual races in groups such as the desmids, the flagellates, and the infusoria, where the whole vegetative organism functions directly as the gamete.

Among the cryptogams, with the exception of the mucors and Marchantia, the sexual relations of the offspring from a single zygote in heterothallic forms, the zygotes of which give rise to more than a single individual, have never been investigated. The condition in the bryophytes has been already discussed under Marchantia. In the thallophytes writers see an alternation of generations variously expressed or suggested in the interpolation of carpospores between the fertilized zygote and the young plant. Whether in the heterothallic oedogoniums, to mention but a single example, the four carpozoospores formed at the germination of the oospore are always all of the same sex, like the germ spores in *Mucor Mucedo*, or may be some male and some female, like the germ spores in Phycomyces, can be decided only by an investigation of the individual thalli which they produce. If species in the Saprolegniaceae and Peronosporeaceae are found to be heterothallic, these forms will likewise furnish a fruitful field for investigation.

The discussion in the foregoing pages is based for the most part upon investigations done or already in progress in the Botanical Institute in Halle. The writer wishes to express his grateful appreciation to Professor KLEBS for the facilities of the laboratory and for his unfailing sympathy in the researches undertaken.

PARIS, April, 1906.

LITERATURE CITED

1. Berthold, G., Die geschlechtl. Fortpflanzung der eigentlichen Phaeosporeen. Mitt. Zool. Stat. Neapel **2**:401–412. 1881.
2. Blakeslee, A. F., Zygospore formation a sexual process. Science N. S. **19**:864–866. 1904.
3. ——— Sexual reproduction in the Mucorineae. Proc. Am. Acad. **40**:205–319. *pls. 1–4.* 1904.
4. ——— Two conidia-bearing fungi, Cunninghamella and Thamnocephalis. Bot. Gazette **40**:161–170. *pl. 6.* 1905.
5. ——— Zygospore germinations in the Mucorineae. Annales Mycologici **4**:1–28. *pl. 1.* 1906.
6. ——— Zygospores and sexual strains in the common bread mould, *Rhizopus nigricans.* Science N. S. **24**: 118–122. 1906.
7. Buchtien, O., Entwickelungsgeschichte des Prothallium von Equisetum. Bibliotheca Botanica **8**: 1887.
8. Campbell, D. H., Mosses and ferns. 1895.
9. Chamberlain, C. J., Alternation of generations in animals from a botanical standpoint. Bot. Gazette **39**:137–144. 1905.
10. Correns, C., Untersuchungen über die Vermehrung der Laubmoose. pp. 472. *fig. 187.* Jena. 1899.
11. Horn, L., Experimentelle Entwickelungsänderungen bei *Achlya polyandra.* Annales Mycologici **2**:208–241. 1904.
12. Klebs, G., Ueber den Einfluss des Lichtes auf die Fortpflanzung der Gewächse. Biol. Centralbl. **13**:641–656. 1893.
13. Küster, E., Vermehrung und Sexualität bei den Pflanzen. Aus Natur Geisteswelt **112**:1–114. *fig. 38.* Leipzig, 1906.
14. Limpricht, K. G., Die Laubmoose. Rabenhorst's Kryptogamen-Flora **4**:2.
15. Prantl, K., Beobachtungen über die Ernährung der Farnprothallien und die Vertheilung der Sexualorgane. Bot.-Zeit. **14**: nos. 46 and 47. 1881.
16. Pringsheim, N., Ueber Sprossung der Moosfrüchte. Jahrb. Wiss. Bot. **11**:1–6. 1878.
17. Schultze, O., Zur Frage von den geschlechtsbildenden Ursachen. Archiv. Mikr. Anat. Entwickel. **63**:197–257. 1903.
18. Stahl, E., Ueber künstlich hervorgerufene Protonemabildung an dem Sporogonium der Laubmoose. Bot. Zeit. **34**: 689–695. 1876.
19. Strasburger, E., Versuche mit diöcischen Pflanzen. Biol. Centralbl. **20**: nos. 20–24. 1900.

A STUDY OF THE VEGETATION OF THE MESA REGION EAST OF PIKE'S PEAK: THE BOUTELOUA FORMATION.

II. DEVELOPMENT OF THE FORMATION.

H. L. SHANTZ.

(WITH SIX FIGURES)

IN an earlier paper[1] the writer has discussed the structure of the Bouteloua formation, and to this publication the reader is referred for general introductory matter. Space will not permit the inclusion here of lists of species in the formations of minor importance, which have to do with the development of this formation. The foothill thicket formation, the plains ruderal formation, and the plains bank formation are each made up of many species. Only the facies and a few of the more important principal species can be mentioned.

Invasion by formations.

FOOTHILL THICKET FORMATION.

This formation extends along the eastern base of the mountains and down along the ridges and gullies far out on the plains. It forms a distinct zone at the base of the mountains (*fig. 8*) and here occurs in its best developed form. In most places under natural conditions there seems to be an ecotone, a place of equal aggressiveness, between this formation and the Bouteloua formation.

FACIES: Cercocarpus parvifolius H. & A., Rhus trilobata Nutt., Quercus novo-mexicana (DC.) Rydb., Q. utahensis (DC.) Rydb., Q. Gambellii Nutt.

PRINCIPAL SPECIES: Rubus deliciosus James, Holodiscus dumosus (Nutt.) Heller, Ribes cereum Dougl., R. leptanthum Gray, R. pumilum Nutt.

In addition to those named there are about one hundred principal and secondary species.

This formation and the Bouteloua formation seldom mix, because where the shrubs grow the facies of the grass formation cannot exist. Nearer the mountains and along the hillsides they alternate sharply.

While the climatic and soil conditions are identical, the differ-

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[1] BOT. GAZETTE **42**:16–47. 1906.

ence in cover causes great difference in physical factors. Simultaneous physical factor readings show very clearly these differences. The following is a typical set:

Aug. 3, 1904, 10:45 a. m.

	LIGHT	TEMPERATURE					REL. HUMIDITY		WATER CONTENT
		Soil	Soil surface	Plant surface	10^{cm}	1^{m}	10^{cm}	1^{m}	
Open............	6s	24°	50°	44°	29°.6	28°.4	40%	32%	3.6%
Thicket (Quercus)	180s	18°	30°	28°.2	27°.2	26°.8	42%	39%	8.3%

FIG. 8.—Zonation at Palmer Park; frontal zone of *Bouteloua oligostachya* and *Artemisia frigida;* zone near base of the bluff *Andropogon furcatus;* at the base of the bluff the foothill thicket (Quercus); the bluff showing pine formation (*P. scopulorum*).

These conditions existed on the same exposures and 6^{m} apart. The open quadrat was dominated by *Bouteloua oligostachya* and *Artemisia frigida;* while the shaded quadrat contained *Quercus utahensis,* *Coleosanthus umbellatus*, *Oryzopsis micrantha*, *Elymus condensatus*, *Filix fragilis*, and *Bryum argenteum*. The thicket was rather open, as may be seen at once by the light readings, the ratio of which is $\frac{1}{30}$. This ratio often becomes $\frac{1}{60}$, but is usually less for the greater part of the formation.

Along the ridges north and east of Colorado Springs there is certain evidence that the thicket formation is slowly pushing its way out into the grass formation. Of the shrubs *Cercocarpus parvifolius* seems best adapted for this invasion, and it is several miles in advance of any of the other dominant species (*fig. 9*). Nearer the mountains evidence is also found of the invasion of the grass formation by the thicket formation. This invasion, however, is not rapid. As soon as the young shrub is established or has grown to sufficient size to produce shade, the grass formation gives way rapidly to species


FIG. 9.—*Cercocarpus parvifolius* invading the Bouteloua formation; pine formation on the horizon.

of the thicket formation. Among the first species to appear in the shade of these advancing shrubs are *Calochortus Gunnisonii, Mertensia linearis*, and *Stipa neo-mexicana*. Later, when the habitat has been rendered less xerophytic and when the other facies have entered, *Coleosanthus umbellatus, Oryzopsis micrantha, Elymus condensatus, Selaginella rupestris Fendleri, Filix fragilis*, and a number of other species appear.

Under perfectly natural conditions and without the intervention of herbivora, the thicket would undoubtedly replace the greater part of the grass near the mountains, but, as is seen later, the thicket is slowly giving way and the grass formation is advancing.

PLAINS RUDERAL FORMATION.

FACIES: Stipa Vaseyi Scribn., Puccinia Stipae Arth., Boebera papposa (Vent.) Rydb., Helianthus petiolaris Nutt., Puccinia Helianthi Schw., Thelesperma intermedium Rydb., Verbena bracteosa Michx., Amaranthus blitoides S. Wats.

PRINCIPAL SPECIES: Salvia lanceolata Willd., Lappula occidentalis (Wats.) Greene, Polygonum aviculare L., Erysiphe Polygoni DC., Munroa squarrosa (Nutt.) Torr., Salsola Tragus L., Euphorbia glyptosperma Engelm., Malvastrum coccineum (Pursh) Gray, Puccinia Malvastri Pk., Vicia americana, Aecidium porosum Pk., Solanum rostratum Dunal, Helianthus annuus L., Cleome serrulata Pursh, Schedonnardus paniculatus (Nutt.) Trelease, Atriplex argentea Nutt., Senecio spartioides Torr. & Gray, Verbesina encelioides (Cav.) Gray, Helianthus petiolaris Nutt., Puccinia Helianthi Schw., Picradeniopsis oppositifolia (Nutt.) Rydb.

The secondary species of this formation are very numerous.

The physical factors of this formation are practically the same as those given for the Bouteloua formation. The conditions of water content are such that the most common ruderals, eastern and European species, cannot thrive to the best advantage. Many native plants behave as ruderals and this name is applied to the formation. This formation represents many different stages in a succession which will result ultimately in the grass formation, and is always invaded by the plants of the grass formation. Only a few of the ruderal species succeed in the grass formation. The most important of these is *Boebera papposa*, occurring everywhere throughout the formation and sometimes very abundant. It is much better developed in a ruderal position and is regarded as a part of the ruderal formation. *Stipa Vaseyi*, another native plant, succeeds best in ruderal positions, but is often found as part of the formation.

The species of the ruderal formation are almost entirely native plants which readily invade any area from which the vegetative covering has been removed. Of the true ruderals, *Salsola Tragus* pushes its way into the formation proper. Here it occurs as dwarfed plants which seldom branch, and which die during the aestival period. *Leptilon canadense*, which occurs only here and there in the ruderal formation, also occurs throughout the grass formation. The plants are usually reduced to 10^{cm} in height.

PLAINS BANK FORMATION.

Whenever a ditch is made through the grass or other formations, or where the grass formation is irrigated, the bank formation comes in. It matters not what kind of soil, the presence of an abundance of water enables this formation to succeed. This, however, is not true invasion, and comes about only as a result of changed conditions which make the existence of the grass formation impossible. Good examples of the coming in of the bank formation may be found in irrigated meadows and in small areas where irrigation ditches or reservoirs have leaked.

A study of this formation is of the greatest interest, for it is along this formation that the eastern species find their way into the region. The reason is obvious, for here they find suitable conditions of water supply. As a result, it is here that the vegetation is made up of the most widely distributed species.

The mountain species find in this formation the cool temperature that enables them to exist away from their natural habitats. These species pass down along the brook banks, while the eastern species pass up along these same banks. The result is a varied flora.

The radical difference in water content between this formation and the Bouteloua formation does not permit of direct invasion. The following species, however, may occur in either formation: *Erigeron flagellaris*, *Agropyron occidentale*, *Helianthus annuus*, *H. petiolaris*.

The facies of the bank formation varies greatly with the age of the formation. In the ultimate stage they are as follows:

Populus deltoides Marsh., P. angustifolia James, P. acuminata Rydb., Salix spp., Prunus melanocarpa (A. Nels.) Rydb., P. americana Marsh., Rosa Sayi

Schwein., Ribes aureum Pursh, Clematis ligusticifolia Nutt., Symphoricarpos occidentalis Hook., Rhus trilobata Nutt.

In an earlier stage this formation is found best developed in the irrigated meadows where *Poa pratensis* L., *Eragrostis alba* L., *Juncus balticus* Willd., *Heleocharis palustris* (L.) R. & S., and *Medicago sativa* L. may rank as facies.

Fig. 10.—Floor of the pine formation (*P. scopulorum*) covered with the Bouteloua formation (*B. oligostachya*, *Koeleria cristata*, and *Artemisia canadensis*).

Xanthium commune and *Melilotus alba* are among the very first plants to enter on a newly formed ditch bank. In this formation are found many of the common species which occur in mesophytic situations in the eastern part of the United States.

PINE FORMATIONS.

As Clements[2] has pointed out, there are two pine formations near the base of the mountain range, the "foothill woodland" and

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[2] Univ. Neb. Studies 4: no. 4. 1904.

the "pine." The first has as facies *Pinus edulis* Engelm. and *Juniperus monosperma* (Engelm.) Sarg.; and as principal species, *Stipa Scribneri* Vasey. The second has as facies *Pinus scopulorum* (Engelm.) Lem. and *P. flexilis* James.; and as principal species, *Arctostaphylos Uva-ursi* (L.) Spreng.

FIG. 11.—*Pinus scopulorum* invading the Bouteloua formation.

In the zone at the base of the mountains lies the foothill woodland formation, while just above is the pine formation. Each of these formations is invading the Bouteloua formation, and the one which lies higher on the mountains, the pine formation, is the more successful.

A consocies of this formation dominated by *Pinus scopulorum* has pushed its way eastward far into Nebraska[3] and carries with it many of the principal and secondary species. *P. flexilis* drops out before the foothills are reached. Near Eastonville, Colo., this formation

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[3] POUND and CLEMENTS, Phytogeography of Nebraska, 2d ed., Lincoln, Neb., 1900, p. 336.

may be seen meeting the Bouteloua formation. All along this ridge the thicket formation has dropped out and the pines advance alone. The forest is not dense, and while many of the principal and secondary species are found on its floor, plants are also found which belong to the grass formation and which are able to survive in this location. In fact, the grass formation is found here in places dominating the floor of the pine formation—a true mixing of the formations (*fig. 10*). This mixing may be due to a certain extent to the entrance of the dominant species of the grass formation, but it is more likely to be the result of the gradual advance of the pines into the grass formation. This is shown very clearly in places where the young pines are several meters in advance of the older trees (*fig. 11*). This invasion may be observed along the ridge leading eastward from Palmer Lake and on which is found the so-called "black forest." Here the pines and the grasses mix and there are no shrubs present (*fig. 10*). The principal species, *Arctostaphylos Uva-ursi*, is also pushing out into the grass formation. A short distance west of Pring, Colo., this pine formation may be seen rapidly advancing along an old roadbed.

An entirely different condition may be observed eleven miles east of Colorado Springs. Here the pine formation is also advancing, but it is accompanied or rather preceded by the thicket formation. The advance of these two formations is favored by the cutting back of the gullies, forming steep hillsides, which offer the most favorable conditions for the growth of these two invading formations.

In many places the thicket, pine, and grass formations are found to meet and mix equally, the grasses forming the floor between the shrubs, and the pine scattered throughout. These three important formations are not only found meeting here on equal terms, but a remnant of an older formation, or at least one which gives evidence of greater age, is also found. This is the foothill woodland. *Juniperus monosperma* is scattered here and there and isolated trees of this species are often found which seem to be very old. Still stronger evidence is found in the fact that here, many miles removed from its fellows, is a very large and apparently very old *Pinus edulis*. Erosion has removed the soil from the base of the tree, exposing the roots, and it is certainly much older than any of the other trees in this region. It is the only tree which supports a rich lichen flora.

Four important formations are found meeting and mixing here: the oldest, the foothill woodland, which has almost disappeared; the pine formation, which is slowly advancing; the thicket formation, which is also gradually advancing; and the grass formation, which gives way as the others advance. The thicket formation at this point entirely lacks the oaks, which fact is probably due to grazing.

In another part of the grass formation there is evidence of a slight advance of the foothill woodland. Young trees of *Juniperus monosperma* have established themselves in a few places on the mesa. In other places *Stipa Scribneri* is entering the plains region along with the thicket formation. The preponderance of evidence, however, seems to be in favor of a recession of this formation, and there is good reason to believe that it was at one time more extensive than at present.

Many species which seem to be most at home in the mountain formations also push down into the Bouteloua formation. Among these may be noted *Achillea lanosa*, extending down the draws, *Geranium caespitosum*, *Gilia pinnatifida*, *G. aggregata*, *Campanula petiolata*, and many other species.

Succession.

PRIMARY SUCCESSION.

On rock.

What the primary succession has been in this region cannot be determined. The succession on rock undoubtedly began with the lichen. On the most exposed rocks of the lime ridge *Staurothele umbrina* and *Lecanora previgna* are practically the only lichens found. On the other rocks the lichens are much more mixed and there seems to be good evidence of the accepted succession for lichens: first the crustose; then the more foliose forms like *Lecanora rubina* and *L. rubina opaca;* and finally *Parmelia conspersa*. On the mesa, where the rocks range from 5^{dm} in diameter to coarse gravel, *Parmelia conspersa* is the most important lichen, although *Rinodina oreina* and *Lecanora calcarea* are also common. *Placo-*

dium elegans, which is also common on rock, seems to require protection and is probably one of the later species to appear. The same may be said of *Lecanora subfusca allophana,* one of the important lichens, which succeeds best in crevices.

The rock lichens occurring within this region belong to the primitive lichen formation.

FACIES: Parmelia conspersa (Ehrh.) Ach., Rinodina oreina (Ach.) Mass.

PRINCIPAL SPECIES: Lecanora calcarea (L.)Sommerf., L. subfusca allophana Ach., L. previgna (Ach.) Nyl., L. rubina (Vill.) Ach., L. rubina opaca Ach., Placodium elegans (Link) DC., Buellia petraea montagnaei Tuck., Lecanora previgna revertens Tuck., L. xanthophana dealbata Tuck., Staurothele umbrina (Wahl.) Tuck.

SECONDARY SPECIES: Placodium cerinum (Hedw.) Naeg. & Hepp., Acerospora chlorophana (Wahl.) Ach., Biatora crenata dealbata Tuck., Heppia Despreauxii (Mont.) Tuck., Placodium vitellinum (Ehrb.) Naeg. & Hepp., Umbilicaria rugifera.

This formation occurs on all exposed rocks, with the possible exception of the Permian, which in most places disintegrates too rapidly to support a lichen flora. With the exception of the last four species, all of the species occur on exposed surfaces. The last four and *Placodium elegans* prefer shaded or at least somewhat protected situations. Throughout the mesa this formation has been almost completely replaced by the Bouteloua formation. On hills and more exposed rocky situations it is sometimes as important as the grass formation with which it alternates. With the more complete disintegration of the rocks this formation will entirely disappear.

On alluvium.

Uncertain as is our knowledge of the primary succession on rock, it is much more certain than our knowledge of the primary succession on alluvium. A careful study of the formation, and in particular those places which are least covered with vegetation, seems to aid in forming an idea of this primary succession.

Near Eastonville, in the region lying between the Bouteloua formation and the invading pine formation, an open area is being invaded by the following species: *Potentilla coloradensis, Thermopsis rhombifolia, Erigeron glandulosa, Paronychia Jamesii;* followed by *Arenaria Fendleri, Muhlenbergia gracilis, Bouteloua oliogostachya,* *Gutierrezia Sarothrae*, *Artemisia canadensis*, and *Tetraneuris glabriuscula*. This is probably the best example of primary succession found by the writer. The absence of ruderal species is especially noticeable.

On the mesa the *Andropogon scoparius* consocies seems to be most primitive. In places not yet covered with vegetation, where the alluvium is nearest what it seems to have been originally, this grass is most abundant and together with *Eriocoma cuspidata* is the first to disappear in passing from this exceedingly open association to the more stable or closed Bouteloua formation. *Eriognum alatum*, *E. Jamesii*, *Tetraneuris glabriuscula*, and *Machaeranthera cichoracea* are generally present; but since they extend into the true Bouteloua formation they are probably not as much a part of the primitive association as the plants mentioned above.

The lime ridge vegetation is probably primitive, as shown by the following quadrat:

Lesquerella alpina	52	Oreocarya thyrsiflora	3
Gutierrezia Sarothrae	5	Gaura coccinea	1
Lithospermum linearis	4	Machaeranthera cichoracea	1

Total surface covered, 5 to 6 %.

At some distance from this, a quadrat shows the following:

Lesquerella alpina	31	Eriogonum Jamesii	3
Grindelia squarrosa	14	Boebera papposa	3
Hedeoma nana	13	Lithospermum linearis	1
Gaura coccinea	8	Salsola Tragus	2
Bouteloua oligostachya	6	Eurotia lanata	1
Aristida longiseta	4	Machaeranthera cichoracea	1
Stipa Vaseyi	3		

Total surface covered, 7 to 8%.

The entrance of Bouteloua is already noted, as is *Aristida longiseta*. A more distant point will show the following quadrat:

Bouteloua oligostachya	54	Lithospermum linearis	6
Atheropogon curtipendulus	28	Aristida longiseta	3
Grindelia squarrosa	16	Eriogonum Jamesii	2
Boebera papposa	57	Pentstemon angustifolius	1
Malvastrum coccineum	7	Salvia linearis	2
Lesquerella alpina	6	Stipa Vaseyi	1
Helianthus annuus	8	Salsola Tragus	2
Gutierrezia Sarothrae	13	Artemisia frigida	3
Chenopodium leptophyllum	10	Evolvulus pilosa	1

Total surface covered, 18 to 20%.

These quadrats are all on steep slopes where the soil is more or less broken. The first quadrat is in pure disintegrated limestone; some gravel has been washed into the second quadrat; while the third is a mixture of gravel, clay, and lime. The difference in soil is of no importance in this connection; since in other places the same succession occurs on the pure disintegrated limestone. In the first quadrat the water content varies from 19 to 6%; in quadrat 3 it varies from 19 to 2%; while in the second quadrat the per cent. of water is intermediate. As one passes from the first quadrat to the second and then to the third, the facies of the Bouteloua formation are found making their appearance; in fact, the flora, aside from a few ruderal species and *Lesquerella alpina*, is decidedly of the Bouteloua formation.

The native species, which are referred to as ruderal, show the greatest ability to occupy new ground and they are the most important in secondary succession. It seems reasonable to suppose that they were also very active in invading the newly formed alluvium, and that, if any of the existing species have taken part in the primary succession, these plants are to be sought among the native ruderals. This can be more clearly understood after a consideration of secondary succession.

SECONDARY SUCCESSION.

The repeated changes which have taken place in the formation of the great plains have manifestly been accompanied by changes in vegetation. What these changes have been can only be inferred from the changes which are now taking place wherever, in the process of erosion, there is a cutting away or deposition of material. These successions in a certain sense are primary, but will be discussed under secondary successions.

Biotic agencies.

There are so many chances for observing secondary successions that the experimental denuded quadrat was not deemed necessary, although several of these are now under observation. There are many trails which lead through the Bouteloua formation where the ground has been but slightly disturbed (*fig. 12*). The travel has simply worn off and killed the original vegetation. After having been in use for a longer or shorter time they are generally abandoned. The soil is hard, in fact has never been broken, but since there is no vegetation, an opportunity is afforded for the entrance of new plants. These trails have not been used in wet weather, and they are therefore never cut up and no loose soil is formed. The succession here is first ruderals like *Boebera papposa*, *Amaranthus blitoides*, or *Verbena bracteosa*. These seem to be most successful invaders of such trails. The grasses of the formation come in slowly, *Muhlenbergia gracillima* generally in advance of, or with *Schedonnardus paniculatus*, *Sitanion elymoides*, *Athero pogon curtipendulus*, and ultimately *Bouteloua oligostachya*. It is not an uncommon thing to find these old trails only distinguishable by the depression of surface and completely covered by the *Muhlenbergia gracillima* consocies. Where the same trail leads through the purer growth of *Bouteloua oligostachya*, it is not so rapidly covered, and when it passes through the *Bouteloua hirsuta* consocies it remains open for a still longer period.

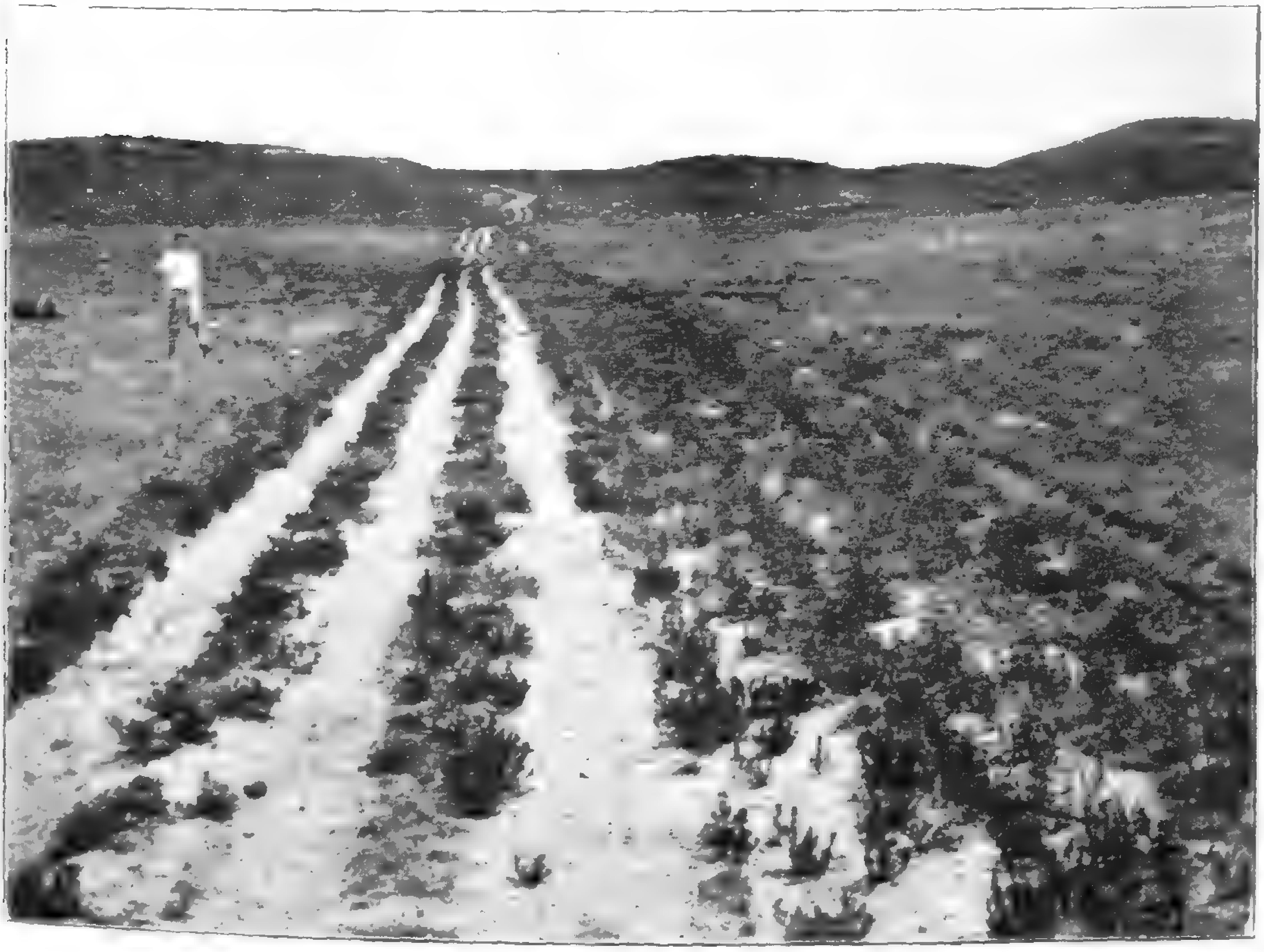

FIG. 12.—Trail invaded by *Boebera papposa;* Bouteloua formation at the sides.

The mesa road was originally of the type just mentioned. During wet weather the road would be cut up to a certain extent and drivers would then turn to one side in order to escape the rough road. The new path has always been formed on the southwest side. This road has been in constant use for several years with the result that plants have been destroyed continually on one side, and have invaded the old roadways from the other. These old roadways show a great many stages in succession.

The road is left in a somewhat roughened condition and the most important species to enter is *Stipa Vaseyi*. It thrives best in newer situations and disappears gradually as one passes back from the well-formed frontal zone. The stable condition which it brings about is not favorable for the growth of the seedlings and it dies out after ten to fifteen years. Aside from the entrance of the annual ruderals *Boebera papposa*, *Amaranthus blitoides*, and *Verbena bracteosa*, it represents the first stage in the succession which will result ultimately in the *Bouteloua oligostachya* formation.

The species which ultimately take possession are usually determined by the adjacent formation. Where *Muhlenbergia gracillima* is dominant it usually appears much in advance of *Bouteloua oligostachya*; but where the latter is dominant, it is usually in advance. *Stipa Vaseyi*, the first perennial to appear, is usually accompanied by the annuals *Boebera papposa*, *Salvia lanceolata*, *Polygonum aviculare*, *Amaranthus blitoides*, and a number of other species. The grasses enter in about the following order: *Schedonnardus paniculatus* followed by *Sitanion elymoides* and *Aristida longiseta*, and ultimately by *Muhlenbergia gracillima* and *Bouteloua oligostachya*. With these grasses there appear many annual ruderals and also the following: *Senecio spartioides*, *Gutierrezia Sarothrae*, *Artemisia frigida*, *Carduus undulatus*, *C. plattensis*, and *Pentstemon angustifolius*.

A transect of the mesa road will give more detailed information regarding the sucessions found here (see transect). This transect is one meter wide. In the plot each division represents one meter, and the most important species in each square meter is placed at the left, and the other species in order of their importance are added to the right.

A, Atheropogon curtipendulus
Aa, Atriplex argentea
Ab, Amaranthus blitoides
Ad, Astragalus Drummondii
Af, Artemisia frigida
Al, Aristida longiseta
B, Boebera papposa
Bh, Bouteloua hirsuta
Bo, Bouteloua oligostachya
C, Calamovilfa longifolia
Ca, Cycloloma atriplicifolium
Cl, Chenopodium lepidophyllum
Cu, Carduus undulatus
Ee, Eriogonum effusum
G, Gutierrezia Sarothrae
I, Iva xanthifolia
L, Lappula occidentalis
Mc, Malvastrum coccineum
Pa, Polygonum aviculare
S, Sideranthus spinulosus
Sc, Sporobolus cryptandrus
Se, Sitanion elymoides
Sl, Salvia linearis
So, Senecio oblanceolatus
Sp, Schedonnardus paniculatus
Ss, Senecio spartioides
St, Salsola Tragus
Str, Solanum triflorum
Sv, Stipa Vaseyi
Te, Townsendia exscapa
Tg, Tetraneuris glabriuscula
Va, Vicia americana
Vb, Verbena bracteosa
Y, Yucca glauca

TRANSECT OF MESA ROAD.

This transect is typical of the greater part of the road. Near Gleneyrie *Machaeranthera cichoracea* appears in abundance in the frontal zone. At the lower end of the mesa road is found considerable variation. *Cleome serrulata* forms the frontal zone, and with this *Boebera papposa, Xanthium commune, Polygonum aviculare, Verbena bracteosa, Munroa squarrosa, Amaranthus blitoides, Solanum rostratum, Chenopodium album*, and *Malvastrum coccineum*. Just back of this, on a portion of the old roadway, is *Stipa Vaseyi*, with *Boebera papposa, Euphorbia dentata, Chenopodium leptophyllum, Ambrosia artemisifolia, Sophora sericea, Polygonum aviculare, Schedonnardus paniculatus, Bouteloua oligostachya, Muhlenbergia gracillima, Artemisia frigida, Xanthium commune, Carduus undulatus, Iva xanthifolia, Asclepias pumila*, and *Salvia lanceolata*. The advance on the graded graveled part is made almost entirely by annuals, *Boebera papposa, Verbena bracteosa, Amaranthus blitoides*, or in rare cases *Solanum rostratum* is most important, while other species are generally present in reduced numbers. The soil in these cases has been packed down and *Stipa Vaseyi* does not enter.

The old mesa road is not followed by the new in all places. In the lower end of the mesa it turns to one side. Here through the original formation, it was only a path. It had been worn down and when abandoned the soil, through the agency of frost and rain, had loosened and fallen in at the sides. This road is now revegetated with *Stipa Vaseyi*, which is in many places replaced by *Muhlenbergia gracillima* and *Bouteloua oligostachya*. In one place this vegetation is practically identical with the formation.

The successions on trails vary considerably in different parts of the region. As one travels from Colorado Springs to Palmer Lake changes are soon noted. A short distance above Colorado Springs *Boebera papposa* becomes less abundant and the first species to invade the roadway is *Plantago Purshii*. Above Monument *Stipa Vaseyi* drops out as an invader, and the principal species which enter are *Polygonum aviculare, Lappula occidentalis, Verbena bracteosa, Amaranthus blitoides, A. retroflexus, Salvia lanceolata*, and *Rumex acetosella*. Below Monument a short distance the following succession was noted: The advancing zone was made up of *Lepidium* *apetalum,Polygonum aviculare*, *Artemisia frigida*, *A. canadensis*, *Verbena bracteosa*, and *Plantago Purshii;* while farther back were found *Bouteloua oligostachya*, *Schedonnardus paniculatus*, *Chrysopsis villosa*, *Arenaria Fendleri*, *Gilia aggregata*, *G. pinnatifida*, *Senecio oblanceolatus*, *Gutierrezia Sarothrae*, *Koeleria cristata*, and *Sitanion elymoides;* followed by the Bouteloua formation in which *Bouteloua oligostachya*, *Stipa comata*, and *Arenaria Fendleri* were most important.

The stages of a succession which converts a denuded trail into the Bouteloua formation are not marked. First there is, as a rule, the entry of many annual ruderal species (*fig 12*). This in many cases is followed by *Stipa Vaseyi*, followed by *Schedonnardus paniculatus*, *Sitanion elymoides*, and *Aristida longiseta*, as well as many other secondary species of the formation, and these in turn by the facies of the grass formation. In some places *Stipa Vaseyi* does not enter and here may be found many other species. Among the more important are *Schedonnardus paniculatus*, *Gutierrezia Sarothrae*, *Chrysopsis villosa*, *Artemisia frigida*, *A. canadensis*, and many other species, followed by the facies of the grass formation.

Near Cheyenne Mountain a number of abandoned corrals show the following as the most important invading species: *Schedonnardus paniculatus*, *Artemisia canadensis*, *Solidago* sp., *Artemisia frigida*, *A. gnaphalodes*, and a number of secondary species—*Petalostemon purpureus*, *Thelesperma gracile*, *Chrysopsis villosa*, *Pulsatilla hirsutissima*, *Lacinaria punctata*, *Sporobolus cryptandrus*, *Aristida longiseta*, *Bouteloua hirsuta*, *Aragallus Lambertii*, and the ruderals *Boebera papposa* and *Euphorbia glyptosperma*.

A denuded quadrat showed during the third summer *Artemisia canadensis*, *Geranium caespitosum*, *Pulsatilla hirsutissima*, *Chrysopsis villosa*, and *Artemisia ludoviciana*. A second corral showed *Artemisia canadensis* and *A. frigida* as the chief invaders, with many other species coming in, of which those most important are *Schedonnardus paniculatus*, *Bouteloua oligostachya*, and *Koeleria cristata*.

The early stages of these successions vary greatly. In the study of a large number the following plants are found to enter first: *Boebera papposa*, in the mesa region and adjacent areas; northward toward Palmer Lake, *Plantago Purshii* or *Polygonum aviculare;*

and farther east *Picradeniospsis oppositifolia*, sometimes accompanied by *Malvastrum coccineum.*

A number of graded roads have been built very recently and these show only the very first vegetation, a ruderal annual vegetation. The boulevard, which runs from Colorado Springs to Manitou, is an older road of this type, having been built for about thirteen or fourteen years. The first permanent succession on this road within the Bouteloua formation was *Stipa Vaseyi*, which is now giving way to *Muhlenbergia gracillima* and *Bouteloua oligostachya.* Many other species came in, among which the more important are *Sitanion elymoides*, *Aristida longiseta*, *Schedonnardus paniculatus*, *Helianthus annuus*, *Quincula lobata*, *Astragalus bisulcatus*, *Sophora sericea*, *Grindelia squarrosa*, with other plants from the formation, as well as ruderal species.

One of the transects of this road deserves special mention. There is a cut here of about 2^{m}, and the road runs north and south. The differences in the east and west sides are due entirely to the differences in exposure, and to its effect upon temperature and water content. The west side, which receives the most light, has first a distinct zone of *Petalostemon oligophyllus*, back of which there is a mixed zone of *Boebera papposa* and *Xanthium commune;* this is followed on the bank by *Stipa Vaseyi*, and this in turn by a crest zone largely of annuals. The east side shows first a zone of *Xanthium commune* followed by *Stipa Vaseyi*, mixed with *Schedonnardus paniculatus*, *Boebera papposa*, *Psoralea tenuiflora*, etc.; and this is followed on the steep unstable soil by annuals. Back of the annuals is the Bouteloua formation in which *Muhlenbergia gracillima* predominates.

There is a great deal of variation in the species which first appear. Almost any one of the species cited under the ruderal formation may dominate in certain places, but the more or less typical examples mentioned above should serve to give an idea of the succession on roads.

Reservoirs are generally built where only one side needs to be dammed. The outer slope of the dam is invaded in the same way a road would be. An interesting exception is found at Palmer's reservoirs. The large reservoir, which was built in 1902, had by

1904 covered the bank chiefly with *Stanleya glauca* and *Mentzelia decapetala.* A great deal of the soil of this bank was hauled in from the lime ridge region, and with it, the seeds of *Stanleya glauca* were carried in. In one of the other reservoirs, which is several years older, *Medicago sativa* was predominant. Normally, *Boebera papposa, Stipa Vaseyi,* and other ruderals would be expected to appear first.

A new reservoir constructed on the mesa in 1904 showed during 1905 the following species: *Boebera papposa, Salsola Tragus, Senecio spartioides, Artemisia frigida, Senecio oblanceolatus, Argemone intermedia, Mentzelia nuda, Polygonum aviculare, P. Douglasii, Euphorbia robusta, Yucca glauca, Chenopodium album, Gaura coccinea, Cleome serrulata, Petalostemon purpureus, Amaranthus blitiodes,* and *A. retroflexus.*

In building roads and reservoirs it often happens that several meters of surface soil and all the vegetation is removed. Succession is different here from the places already mentioned. The annual ruderals do not appear in such great numbers. Among the species which enter are *Argemone intermedia, Mentzelia ornata, Petalostemon oligophyllus, P. purpureus, Sitanion elymoides, Aristida longiseta, Munroa squarrosa,* and other common hillside plants, since the soil here is usually gravel.

Broken areas.

Here and there on the plains are found areas which have been plowed and planted, but have been abandoned because of the scanty water supply. The succession of plants here is much the same as on graded roads, but is usually more uniform. An abandoned garden patch showed the following year the facies *Anogra albicaulis,* with *Chenopodium album* and *Helianthus annuus* as the principal species. An area on top of the mesa showed almost a pure stand of *Boebera papposa;* while still another showed *Schedonnardus paniculatus. Artemisia frigida* sometimes enters denuded areas and dominates the early stages of the succession. During 1904 a tract was seeded with *Lolium perenne;* the following summer it showed *Boebera papposa* and *Verbena bracteosa,* as well as *Polygonum aviculare, Salsola Tragus, Artemisia frigida, Lolium perenne,* *Solanum triflorum*, *Senecio oblanceolatus*, and *S. spartioides;* also a very few young plants of *Yucca glauca*, *Argemone intermedia*, *Carduus undulatus*, and *Tetraneuris glabriuscula*.

The usual flora on the hills of the prairie dog is *Anogra coronopifolia*, *Malvastrum coccineum*, *Munroa squarrosa*, *Amaranthus blitoides*, *Picradeniopsis oppositifolia*, *Boebera papposa*, and *Artemisia frigida*. *Muhlenbergia gracillima* is the most effective in reclaiming the old deserted hills. In fact, in looking over a deserted dog town the location of the old dog hills can be determined at once from the fact that although the surrounding vegetation is dominated by *Bouteloua oligostachya*, the location of the old hills is marked by a community of *Muhlenbergia gracillima*.

Near Pring, Colo., an abandoned field showed the first year *Helianthus petiolaris*, with a less amount of *Boebera papposa*, *Malvastrum coccineum*, *Solanum rostratum*, *Lappula occidentalis*, *Verbena bracteosa*, and a very few plants of *Artemisa frigida*, *Atheropogon curtipendulus*, *Schedonnardus paniculatus*, *Carduus undulatus*, and *Eriogonum annuum*. Here are found three very distinct sets in the succession. First, annual species, followed by a group of ruderal species, and this in turn by perennials from the Bouteloua formation. In another place *Thelesperma intermedium* was the first species to enter. Near Falcon, Col., an abandoned field showed after two years *Helianthus petiolaris* and also *Munroa squarrosa*, *Lappula occidentalis*, *Chaetochloa viridis*, *Plantago Purshii*, *Amaranthus retroflexus*, and *Ptiloria ramosa*. In some places *Bouteloua oligostachya* was entering. Another field which had been abandoned for about eight years showed *Sporobolus cryptandrus*, *Aristida longiseta*, *Schedonnardus paniculatus*, *Cenchrus tribuloides*, as well as *Senecio oblanceolatus* and *Munroa squarrosa*, a few annuals, the more important of which were *Helianthus petiolaris*, *Verbena bracteosa*, and *Cryptanthe ramosissima*. Into this area *Bouteloua oligostachya* was pushing its way and had in places near the edge of the field almost replaced the other species.

Several miles west and south of Fountain, Col., a most interesting stage of succession is shown. The surrounding vegetation is of the *Bouteloua oligostachya* consocies with very few primary and secondary species. An area which had been broken and abandoned showed the *Muhlenbergia gracillima* consocies almost entirely replacing the earlier stages of the succession. A very little *Boebera papposa* and *Schedonnardus paniculatus* remained, while about an equal amount of *Bouteloua oligostachya* was invading and will after a number of years replace the Muhlenbergia.

As long as the ants are alive, they remove all vegetation for some distance around their hills. In low places *Cleome serrulata* may form a semicircular zone on the lower side of this denunded area. *Helianthus annuus*, *H. petiolaris*, *Stipa Vaseyi*, and many other species may also be found in this situation. The most common plant to develop in this area is *Munroa squarrosa*, which often forms a perfect zone.

Erosion.

The dry soil is easily washed away by heavy rains. This forms loose soil at the base of the hills and also leaves broken places from which the soil is removed. On the hillsides there are often produced natural terraces, each of which ends in a broken edge. During the rains these terraces are cut back and new soil is exposed. These places may be occupied by *Boebera papposa*, *Salsola Tragus*, or other annuals, but generally *Stipa Vaseyi* is the invading species. Here it serves to bind the soil and prepare the way for *Muhlenbergia gracillima* and *Bouteloua oligostachya*.

In the low draws there is generally a hollow washed out below the terrace, and as a result of the falling in of the soil when dry there is found both loose and undisturbed soil. These places are marked by a growth of *Stipa Vaseyi*, with *Boebera papposa*, *Solanum rostratum*, and often *Salvia lanceolata*, *Helianthus annuus*, *Verbena bracteosa*, *Salsola Tragus*, *Xanthium commune*, and *Leptilon canadense*. Places such as this are very much like the ordinary draw where more or less of the soil which was washed down from the hills is deposited. Conditions here are also almost the same as in the alluvial fans which are formed at the bases of all the ravines, whether they be small or large. Here new soil is deposited during every heavy rain, and as a result the slow growing grasses such as *Bouteloua oligostachya* and *Muhlenbergia gracillima* cannot thrive. *Stipa Vaseyi* is the most successful plant of such habitats. It marks the dry water courses and also all of the alluvial fans. Succession here is practically the same as on any ruderal area. In addition to *Stipa Vaseyi* there is usually found *Boebera papposa*, *Salvia lanceolata*, and in some cases *Xanthium commune* and *Cleome serrulata.* When the soil has become more stable *Stipa Vaseyi* slowly gives way. *Artemisia frigida* is now one of the first species to appear, and is often dominant after *Stipa Vaseyi* has disappeared entirely. This is followed by *Muhlenbergia gracillima*, and after a number of years this is replaced in turn by *Bouteloua oligostachya.*

FIG. 13.—Blow-out; the prominent plants are *Muhlenbergia gracilis*, *Meriolix serrulata*. *Artemisia canadensis*, and *Andropogon scoparius*; *Calamovilfa longifolia* in the background.

On dry sandy ridges blow-outs are often found (*fig. 13*). The succession here is usually *Polygonella articulata*, *Cycloloma atriplicifolium*, *Carex* sp., *Muhlenbergia gracilis*, *Sporobolus cryptandrus*, *Artemisia canadensis*, *Thelesperma gracile*, *Eriogonum annuum*, *Meriolix serrulata*. *Chrysopsis villosa*, and *Andropogon scoparius.*

The most important plant occupying the alluvium deposited by permanent streams is *Melilotus alba.* Species of minor importance are *Juncus bufonius* and *Riccia crystallina.*

ANOMALOUS SUCCESSION.

When biotic or physical agencies bring about sufficient change in the habitat, the result is an anomalous succession. The change of habitat may be gradual and yet the effect on the succession be such as will change entirely the ultimate formation. We may also have the succession interfered with in such a way as to hasten the ultimate formation, to cause it to become more stable in a shorter time, or to retard the succession or reduce it to a more primitive condition.

Due to grazing.

The influence of grazing is very clearly seen by comparing fenced areas with those that have not been protected from grazing animals. Cattle, and to a less extent horses, are the only animals that have grazed within this region in recent years.

Near the lower end of the mesa is Colorado City, the old territorial capital of Colorado and known as one of the oldest towns in the state. For fifty years it has been the custom to have a herd boy drive the cattle out on the adjacent areas to graze each day and bring them back each night. Colorado Springs, a more recent city, also sends its herds out on the same area. It will be well, at first, to see what effect this has had upon the Bouteloua formation. In those parts of the formation where grazing has not played a part the formation is very open, while in the grazed portions it is more closed. In the open formations many species appear with the grasses, while in the more closed formation these species are almost entirely absent. A typical quadrat from the south mesa which has been grazed shows the following species:

Muhlenbergia gracillima	23	33%	Sideranthus spinulosus	3
Bouteloua oligostachya	24	12	Malvastrum coccineum	5
Atheropogon curtipendulus	1		Townsendia exscapa	2
Artemisia frigida	2		Echinocereus viridiflorus	1
Boebera papposa	36			

Total surface covered, 45 to 50%.

In some of the draws the preponderance of *Muhlenbergia gracillima* is even more marked. Near the above quadrat, in a portion protected from grazing, a quadrat would show:

Bouteloua oligostachya	18 %	Artemisia frigida	1
Muhlenbergia gracillima	2.5	Artemisia gnaphalodes	1
Aristida longiseta	2.5	Gutierrezia Sarothrae	2
Chrysopsis villosa	8	Sitanion elymoides	1
Thelesperma gracile	9	Eriogonum alatum	2
Echinocereus viridiflorus	4	Pentstemon angustifolius	1
Opuntia polyacantha	3	Carex pennsylvanica	5
Euphorbia robusta	1		

Total surface covered, 27%.

In a portion of the mesa which has been grazed, but not to such an extent as the first quadrat given, is found:

Bouteloua oligostachya	22%	Artemisia frigida	5%
Muhlenbergia gracillima	7		

It cannot be stated positively that this condition is entirely due to grazing. It seems likely, however, that grazing would favor the development of grasses and tend to destroy the other plants, particularly the dicotyledons. There is a very noticeable difference in adjacent areas when one is protected from grazing. The preponderance of *Bouteloua oligostachya* and *Muhlenbergia gracillima*, and the paucity of higher spermatophytes in the grazed area is the chief difference. This seems to be the exact condition which would come about by natural succession and the grazing in this case hastens this succession. The more primitive parts of the formation and those which have not been grazed are much alike. Grazing, when not too severe, favors the development of the facies of the formation.

Still another condition due to grazing should be considered. Near Colorado City, and particularly in the region lying between Colorado City and Colorado Springs, the grazing has been very severe. The result here has been first to drive out most plants other than the grasses, and ultimately even to destroy *Bouteloua oligostachya* and *Muhlenbergia gracillima* to a great extent. A few plants, such as *Astragalus bisulcatus*, *Chrysothamnus graveolens*, *Grindelia squarrosa*, and others which are not touched by grazing animals, still survive; but the character, aside from a few of these species, is now almost entirely marked by annuals. The succession has become practically that which follows on a denuded area. *Salvia linearis, Atriplex argentea,* and *Bouteloua prostrata* are here the principal species. With these are found many of the ruderal plants as well as the following important perennials: *Agropyron occidentale, Astragalus bisulcatus, Sophora sericea, Vicia americana,* and a very little *Bouteloua oligostachya, Quincula lobata,* and *Phyllopterus montanus.*

The effect is to delay the succession or to cause it to return to a more primitive condition. The grazing does not change the Bouteloua formation into another formation, since grasses seem to be especially adapted to these conditions.

The effect of grazing is very different on the thicket formation. Wherever cattle are allowed to crop the thicket formation very closely, the facies are completely killed. This is the most noticeable in the case of the oaks, which are killed by the entire loss of chlorenchyma tissue. They are attacked by cattle before any of the other facies of the thicket formation.

An examination of the region shows that on the mesa near Colorado City the thicket formation has been replaced almost entirely by the Bouteloua formation. Only scattered bushes of *Cercocarpus parvifolius* and *Rhus trilobata* are found and these much reduced in size. The explanation lies in the fact that this portion has been grazed more than the part which is farther removed from Colorado City. The remnant of the old thicket can be seen in many places, and the stages in the succession which have produced a grass formation instead of a thicket formation may be traced. There is a scanty plant growth under these shrubs. When they are killed outright the space is open to plant invasion, and as a result the ruderals come in in abundance. *Chenopodium album* may be one of the forms which appears at this time, especially if the cattle have destroyed most of the under vegetation. At other places where the shrubs have been cut down the succession may be much the same as the ruderal succession and result in the typical Bouteloua formation. As a rule the shrubs are gradually reduced in size. The result here is that the grasses slowly encroach upon the area as the shrubs are eaten lower, and as the clump becomes more open the undergrowth increases. *Agropyron occidentale, Stipa comata, S. neo-mexicana, Atheropogon curtipendulus* come in slowly; *Coleo-*

santhus umbellatus and *Chenopodium Fremontii* disappear. When the shrub ultimately dies and breaks up, there is a very small ruderal place in which the succession is identical with that already described for denuded places. Grazing changes the thicket formation to a grass formation, and the more rapid the change the more nearly it approaches the ordinary ruderal successions.

Due to drainage.

Drainage is not an important factor, but it seems best to consider here those changes which result when an irrigated area is left without irrigation, a ditch abandoned, or the water of a stream turned aside causing the bed to become dry.

Examples of the first case mentioned are not found excepting where, because of lack of attention, the water does not flow evenly over a meadow. The succession here is gradual, forms like *Erigeron flagellaris*, *Vicia americana*, and *Astragalus hypoglottis* taking the place of the more hydrophytic grasses and rushes. If the change of habitat is abrupt, most of the species die and a ruderal succession follows. When the change is very gradual, the species mentioned above, together with *Agropyron occidentale*, take the place of the rushes. *Bouteloua oligostachya* often appears in this stage of the succession, but *Muhlenbergia gracillima* is one of the last to appear.

In abandoned ditches a mixed formation is generally found. In this habitat the following species of the mesophytic bank formation may continue for a long time: *Clematis ligusticifolia*, *Xanthium commune*, *Symphoricarpos occidentale*, *Stachys palustris*, *Erigeron flagellaris*, and *Vicia americana*. The last two species are elements of the Bouteloua formation and are able to adapt themselves to the change of habitat. Of the grasses of the Bouteloua formation, *Bouteloua oligostachya* and *Agropyron occidentale* are the first to enter. They appear much earlier than *Muhlenbergia gracillima*, and thrive even better in these transformed ditches than in the Bouteloua formation proper.

There is only one example of the effect of a change in the natural water course. This is not complete, but enough water has been taken from Camp Creek to cause it to be dry for a greater part of the year. The first and most noticeable effect has been the death of the trees, *Populus angustifolia* and *P. deltoides.* This condition has obtained for only about three years, and the effect thus far has been destructive. The bank species, with the exception of those that are able to exist in more xerophytic habitat, have died, and aside from the entrance of a very few ruderals there has been no marked succession as yet.

Due to irrigation.

The changes produced by irrigation are complete and varied. Where a ditch passes through the Bouteloua formation in places where there is seepage, the first stages of the succession which lead to the irrigated meadow formation are found. The effect here is usually the better development of *Agropyron occidentale*, and at the same time the disappearance of *Muhlenbergia gracillima. Bouteloua oligostachya* also grows more rank than where not irrigated. This succession is exceedingly variable, probably because of the variable water supply, and the stage of the succession is an index to the amount of water added. In some places the meadow flora is reduced largely to rushes and other hydrophytic plants, while in other places *Bouteloua oligostachya*, *Erigeron flagellaris*, *Vicia americana*, and *Astragalus hypoglottis* are most important.

In the bank formation the conditions are varied. Between the water and the xerophytic formation through which the stream or ditch runs, there are all gradations from hydrophytic to xerophytic. But to divide this formation in regard to water content of the soil would not be practicable. Another condition makes the formation more complex. In the ditch formation, there is, besides the invasion of the mesophytic and hydrophytic plants, the entrance of the ruderal. When the ditch is first made the ruderal formation makes its appearance. At almost the same time the mesophytes and hydrophytes appear. The ruderal formation always tends towards self destruction. Here the result is that the outer portion of the ditch is ultimately occupied by the characteristic Bouteloua formation, while on the inner the more mesophytic bank species become established. In the ultimate bank formation the line of separation from the grass formation is very distinct.

Along many of the irrigation ditches a condition prevails which prevents the development of the ultimate stage of the succession. Each year the bottom of the ditch fills up with silt which is removed to the bank the following spring. This forms a new soil for the entrance of ruderal species, and as a result the bank returns to a somewhat primitive condition.

Another factor of importance here is the fact that during the winter the ditch is empty the greater part of the time. This condition is detrimental to the success of the species of the ultimate formation. The result is that along these irrigation ditches are found various stages of anomalous successions, which are checked repeatedly, or even turned back by the reversion to more primitive conditions. The successions are interrupted again and again, and this may account to a great extent for the variable character of the bank formation.

General discussion.

After careful study it is at once apparent that all parts of the formation are not of the same age. The secondary successions throw much light upon the structure as well as upon the development of the formation. These exhibit rather well-marked stages. The first is a ruderal consocies; the second, a society of the formation; while the ultimate stage is a consocies of the formation. All of these successions lead undoubtedly to the Bouteloua formation.

The successive deposition and erosion which has produced the Great Plains does not differ markedly from that which may be noted at the present time. The vegetation on new deposits of soil passes through the typical succession leading from the ruderal to the grass formation. Near the mountains the cutting back of the gullies results in the establishment of the thicket formation, which is preceded usually by the entrance of many of the secondary species of the thicket and grass formation. The pine formation is usually mixed with the thicket formation. When this cutting back of the gullies exposes rocks of a sufficient degree of stability, the primitive lichen formation precedes all others.

In many places gullies are cut back which are reclaimed at once by the grass formation. The thicket and pine formations do not enter. In these places the *Andropogon scoparius* consocies usually becomes established.

The elevated dry ridges are occupied by the *Selaginella densa* formation in which *Paronychia Jamesii* is a prominent species. This evidently represents a younger stage in a succession which will give ultimately the Bouteloua formation. Among the most important invading species are *Stipa comata*, *Koeloeria cristata*, and *Bouteloua hirsuta*.

If these ridges are sandy, blow-outs often occur which result when reclaimed in the *Calamovilfa longifolia* consocies (*fig. 13*). This consocies thrives much better when not grazed. Grazing changes it to the Bouteloua consocies.

The *Andropogon scoparius* evidently represents an earlier stage in the formation than the *Andropogon furcatus* or *Bouteloua oligostachya* consocies. It occurs on the hillsides and also is found as an early stage in the succession on denuded xerophytic areas. The study of secondary succession would lead also to the belief that *Muhlenbergia gracillima* is only a stage, for here it is replaced repeatedly by *Bouteloua oligostachya*.

The societies of the formation are, without exception, dominated by species which are among the first to invade new areas. Their presence in the formation is largely due to historical reasons. To this may be added the fact that the consocies which represent the earlier stages, as for example the *Bouteloua hirsuta* consocies, have by far the greater number of societies.

The *Bouteloua oligostachya* consocies represents the ultimate stage of the grass formation and is by far the most widely distributed of any of the consocies of the formation.

This study of the Bouteloua formation was suggested by Professor FREDERIC E. CLEMENTS, under whose direction it has been carried on. To him and also to Professor CHAS. E. BESSEY the writer wishes to express his thanks for many helpful suggestions and criticisms. Thanks are also due to the following persons: Professor F. D. HEALD, for advice and criticism; Professor WM. STRIEBY, for generously giving me use of his laboratory for the determination of water content; and to Professor F. H. LOUD, for meteorological data.

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CORTINARIUS AS A MYCORHIZA-PRODUCING FUNGUS[1]

C. H. KAUFFMAN.

(WITH ONE FIGURE)

THE study of the mycorhiza problems has received a new impetus during the last six years by the appearance of extensive papers by MACDOUGAL (**1**), STAHL (**2**), TUBEUF (**3**), HILTNER (**4**), and MÜLLER (**5**). Considerable evidence has been adduced showing that in the case of the endotrophic mycorhiza the organisms concerned act as purveyors of nitrogen to the symbiont or host with whose roots they are connected (**6–7**); furthermore, the organisms in some of these cases have been quite exhaustively studied (**8–9**). On the other hand, the fungi which cause the ectotrophic mycorhiza have not been investigated except in a very few cases.

It is a noticeable fact as one looks over the literature, that the larger part of the work hitherto attempted has been done on a basis of several unknown quantities. One of these is the identity of the fungus which causes the ectotrophic mycorhiza. The earlier writers speak of the fungus as if it were a single species or genus. It was thought for quite a time that the ectotrophic mycorhiza of European trees was due in all cases to the tubers or truffles. WORONIN (**10**), in 1885, showed that this cannot be true for Finland, where the tubers are not found, but where nevertheless the mycorhiza are abundant. KAMIENSKI(**11**) also found no truffles in the regions where he studied the mycorhiza of Monotropa. REES (**12**) was at first inclined to think that Elaphomyces was the cause of the mycorhiza of almost all the trees he examined; later, he himself found mycelium of mycorhiza which differed in structure from that of Elaphomyces.

The fungi whose fruiting forms have been definitely reported as belonging to mycorhizal mycelium are comparatively few. MACDOUGAL (**1**) gives a list of mycorhizal fungi whose identity has been reported. The list is as follows: Fusisporium, Eurotium, Pythium, Nectria, Celtidia, Elaphomyces, Geaster, Boletus, Tricholoma, Lactarius, and Cortinarius. Of the non-mycelioid forms

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[1] Contribution 89 from the Botanical Department of the University of Michigan.

which are known, *Phytomyxa leguminosarum* and Frankia are of course the most prominent. It will be seen that the list is remarkably small, especially if we remember that only one or two species is referred to in each case. As we are only concerned with ectotrophic forms, the first four can be omitted in the discussion, and if we consider the evidence on which the symbiotic connection of the remainder is based, we find the actual list even smaller.

In the case of the Boleti, WORONIN (**10**), after declaring the tubers out of the question, says: "Vielleicht gehört die hiesige Mycorhiza einem anderen, ebenfalls unterirdischen Pilze an, dies will ich nicht bestreiten, bin aber vielmehr geneigt anzunehmen, dass die oben angeführten Boleten mit der Mycorhizen zusammenhängen." It seems that WORONIN himself was not very certain of the connection. Elaphomyces was very exhaustively studied by REES (**11**), who showed that it is undoubtedly connected with the pines in localities where the truffle occurs. Two species of Geaster, *G. fimbriatus* and *G. fornicatus*, were shown by NOACK (**13**) to be attached to the roots of the spruce and pine.

When we come to a consideration of the agarics our knowledge is meager indeed. Only one investigator, NOACK (**13**), in 1889, has concerned himself with them. He found that five species of this group were apparently mycorhiza-producers on the forest trees of the locality where he made his observations. Two were Tricholomas; one a Lactarius; and three were Cortinarii. He merely makes the bare statement that they are connected with the rootlets by their mycelial strands, which he could easily make out. It is very probable that his observations are correct.

It seems to be appreciated that we need some investigation to determine what fungus we are dealing with, so that problems which have to do with the physiological side of mycorhiza may be undertaken more intelligently; for it is just as likely that knowledge concerning the fungus and its life history may lead to an understanding of the relation of the two organisms as a knowledge of the tree would. It seemed worth while, therefore, to report the identity of any such mycorhizal fungi whenever the evidence seemed sufficient to make it acceptable.

OBSERVATIONS ON **Cortinarius rubipes,** sp. nov.[2]

In a previous paper (**14**) I pointed out that the members of the genus Cortinarius were so constantly found in limited areas, and some species in such close proximity to certain trees, that it seemed likely that there was some connection. This last summer an effort was made to find out to what extent this might be true. The season was wet during the early summer, and although one finds few Cortinarii as a rule before August, several did occur, and one of these proved to be favorable for my purpose. It not only showed beautifully its connection with the tree roots, but turned out to be an undescribed species of Cortinarius.

FIG. 1.—*Cortinarius rubipes*, sp. nov.—Left hand sporophores show the mass of rootlets and humus with strands of mycelium projecting above; right hand individual shows the roots with the short mycorhizal branches and the mycelial strands which are attached to the base of the stipe.—Photographed by the writer.

It was found July 4, 1905, on the south slope of a small ravine along the Huron River, near Ann Arbor, in a layer of humus and forest leaves. This species, as is indeed true of some other fleshy fungi, is characterized by its brick-red mycelial strands and stem. By removing the surface soil it was possible to see the brick-red strands intertwining with the rootlets apparently in all directions.

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[2] For description in full, see 8th Report Mich. Acad. Sci. 1906.

But it was soon found that the reddish network extended along definite paths. Beginning with a tiny rootlet, the fungus was followed to a rather large root, apparently growing from a hickory. On examination, however, it was found that the mycorhiza-bearing root passed the hickory, and that all the roots of the hickory examined were devoid of a colored mycorhizal fungus. On the other hand, the root in question was now easily traced to a clump of red oaks, of second year growth, which were distant at least 54^{dm} from the starting point. Besides the hickory, the roots of a Crataegus which crossed the oak roots were likewise devoid of the fungus in question.

The red strands were attached only to the small rootlets, and where the roots extended below the black soil into the yellow subsoil the mycorhiza gradually disappeared, facts which were known to FRANK, STAHL, and others. The leaf mold along with the remains of last year's leaves forms a thin covering beneath which the young buttons of the fungus are started.

About twenty paces down the slope, another troop of the same species of Cortinarius was found. These came up only 30^{cm} away from a fine young sugar maple and close to one of its main roots. Expecting that they were probably attached to the roots of an oak a short distance away, I dug down carefully and found to my surprise that the strands which were very luxuriant here were attached to the rootlets of the sugar maple; even the small roots growing directly from the base of the trunk were thickly beset by the strands. The sporophores were loosened and the attachment of the strands followed from the stipe to the rootlets and thence to the tree. Several days later on visiting the same hill, two more sporophores were found on the north slope of the hill, again with the characteristic strands, and connected with a red oak.

I had to leave Ann Arbor at this time, and not until I came back in September did I have any further opportunity to make observations. On October 30 the slope was dug over for a considerable area around the original habitat of the Cortinarius in question. The roots of the same maple were found to be hung with the reddish strands in all directions, just as luxuriant apparently as in the early summer. Here, also, other roots crossing or intertwining with the maple roots—with one exception—were not affected by the fungus.

An ash, basswood, and white oak were examined, but no trace of the fungus found. About 27^{dm} from the sugar maple, it was found that some of the strands were apparently attached to a different root. Following this up to a clump of red oaks about 54^{dm} away, I was again surprised to find that the oak roots in this case were not connected with the fungus at all, but that the root which was followed —which did not have the appearance of an oak root—belonged to a large *Celastrus scandens* which wound around one of the oaks. It was clear that we had another symbiont connected with the fungus.

DISCUSSION

It may be well here to call attention to the following points which have been brought out: (*a*) that *Cortinarius rubipes* (for so we will call it) is connected with three forest symbionts belonging to different families; (*b*) that it is apparently selective in the sense that the specific character of the symbiont does not necessarily attract it; (*c*) that one of the symbionts is a maple.

NOACK (**12**), who has been the only investigator of the agarics as producers of mycorhiza, thinks he has connected *Tricholoma terreum* with both beech and fir, and *Lactarius piperatus* with beech and oak. My own observations seem to show that it is undoubtedly a fact that one fungus may be attached to trees of very different families. In the case of *Celastrus scandens* no fruit bodies were seen, but there can hardly be a doubt that it was the mycelium of the same species.

It is rather unexpected to find that the same tree species when exposed to the fungus does not always become associated with it. It is evident that the mycorhizal fungus may attach itself to very different hosts, dependent for its initial attachment on certain environmental factors.

The maples of Europe are reported as seldom forming mycorhiza (**2**). The roots of the sugar maple mentioned above were carefully examined with a lens, and also under the microscope, and mycorhiza seemed to be everywhere abundant on the smaller rootlets. How generally they occur on our maples is not known, as hardly any work has been done in this line in our country.

With regard to the kind of mycorhiza involved, there is of course no uncertainty. Some of the strands and the connected rootlets were fixed and imbedded, and sections were made to determine the more intimate relations of the two organs. When stained rather deeply by fuchsin and gentian-violet the connection could be easily made out. It is clearly a true ectotrophic mycorhiza. There is a close-lying layer of parallel hyphae which surrounds the rootlet, and, in all but the youngest rootlets, branches of this layer penetrate the root and form a close intercellular tissue exactly as figured by FRANK (**13**). The cells of the root at this time seem to contain little protoplasm and occasionally hyphal threads are seen to cross the cells of the cortical layer farther in. In the youngest roots no intercellular tissue appears to be present.

It would seem that there must be some close physiological relation; FRANK indeed thought he had demonstrated it. At the present time, however, nothing definite is agreed upon. To attempt in some measure to solve this question, experiments are now under way with the mycelium of the above-mentioned mushroom. One fact may have some bearing on the problem; the species of the genus Cortinarius develop relatively slowly. The writer has never been able to bring buttons into the house and develop them there, as is possible with Amanitas and Volvaria. For some reason they seem to have lost the vigor necessary to this end. It may be that the explanation of this is found in that a part of their food supply is cut off, and that the tree really supplies some of the necessaries for the full development of the sporophore.

Let it not be supposed that all Cortinarii are mycorhiza-formers, at least normally. *Cortinarius armillatus*, for example, although very partial to *Tsuga canadensis*, is usually found among rotten logs or leaf-mold near this tree, and is probably a saprophyte; on the other hand, it has been found growing out of a cleft at the base of one of these hemlock trees. It seems quite likely, however, that a good many Cortinarii are in symbiotic connection in the manner of the one described in this paper. During several seasons' observations, I have found *C. squammulosus*, *C. bolaris*, and *C. cinnabarinus* again and again in places which would indicate some relation to one kind of tree. *C. cinnabarinus* seems to prefer the oak, the other two the beech. NOACK (**12**) has shown the connection of *Cortinarius callisteus* with the beech, *C. caerulescens* with the beech, and *C. fulmineus* with the oak. Others will no doubt be added to the list as soon as observers enter this interesting field.

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LITERATURE CITED.

1. MACDOUGAL, D. T., Symbiotic saprophytism. Annals of Botany **13**: 1. 1899.
2. STAHL, E., Der Sinn der Mycorhizenbildung. Jahrb. Wiss. Bot. **34**: 539. 1900.
3. TUBEUF, K., Beiträge zur Mycorhizafrage. Naturwiss. Zeitsch. Land. Forstwirts. **1**: Feb. 1903.
4. HILTNER, L., Beiträge der Mycorhizafrage. Idem **1**: Jan. 1903.
5. MÜLLER, P. E., Über das Verhältniss der Bergkiefer zur Fichte in den Jutländischen Heideculturen. Idem **1**: Aug. & Oct. 1903.
6. HELLRIEGEL H. & WILFARTH H., Untersuchungen über die Stickstoffernährung. Ber. Deutsch. Bot. Gesells. **7**: 138 and footnote. 1889.
7. NOBBE & HILTNER, Die endotrophe Mycorhiza von Podocarpus und ihre physiologische Bedeutung. Landwirts. Versuchsst. 51. 1899.
8. ATKINSON, G. F., Contribution to the biology of the organism causing leguminous tubercles. Bot. Gaz. **18**: 157, 226, 257. 1893; and literature quoted.
9. SHIBATA, K., Cytologische Studien über die Endotrophen Mycorhizen. Jahrb. Wiss. Bot. **37**: 643. 1902.
10. WORONIN, M., Über die Pilzwurzel von B. Frank. Ber. Deutsch. Bot. Gesells. **3**: 205. 1885.
11. REES, M., Über Elaphomyces und sonstige Wurzelpilze. Ber. Deutsch. Bot. Gesells. **3**: 294. 1885.
    ——— Über den Parasitismus von *Elaphomyces granulatus*. Bot. Zeit. **38**: 729. 1880.
12. NOACK, Über Mycorhizenbildende Pilze. Bot. Zeit. **47**: 389. 1889.
13. FRANK, B., Ber. Deutsch. Bot. Gesells. **3**: *pl. 10*.
14. KAUFFMAN, C. H., Bull. Torr. Bot. Club **32**: 301. 1905.

A NEW FUNGUS OF ECONOMIC IMPORTANCE.

RALPH E. SMITH AND ELIZABETH H. SMITH.

(WITH THREE FIGURES)

AMONG the subjects of investigation by the California Agricultural Experiment Station, that of a destructive rotting of lemons occurring in southern California is one of the most important. The cause and means of control of this rot have been a complete mystery to the handlers of lemons, and the fact that the trouble has been found to be due to a fungus representing not only a new species, but a well-defined new genus, makes the case one of peculiar interest.

The rot in question has been called the "brown rot," distinguishing it from the "blue mould," or Penicillium rot, the commonest form of Citrus decay. The latter has been known since time immemorial, but with the best class of lemon shippers is not usually a great pest. Lemons affected by Penicillium are almost invariably those which have become bruised in handling or subjected to improper conditions. With fruit properly handled, cases of blue mould are only occasional. In these the affected lemon decays and becomes covered with the dusty fungus, finally collapsing into a slimy mass, without infecting the other fruit, even though they be covered with the spores. A Penicillium-affected lemon in the midst of a box does not usually infect the other fruit about it in the least when proper conditions are maintained.

Within the past few years a new and much more serious form of rot has been detected by the lemon growers and shippers. In lemons which had been picked, washed, and stored for curing, it was found that a rot developed which spread rapidly by contact through the fruit, soon involving the entire box if left undisturbed. In appearance the affected lemons are characteristic and easily distinguished from those affected by blue mould, though the latter fungus follows rapidly on the other and soon covers the decaying fruit. Particularly characteristic is the odor of lemons affected by brown rot, a peculiar rancid smell by which an experienced person can detect one affected lemon in a large amount of fruit. This odor has, in fact, come to be the infallible test for brown rot in the lemon curing houses, readily distinguishing the trouble from all other forms of decay. The rapid spread in the box by contact, and the appearance of affected fruit, are also very characteristic, though the latter is soon disguised by Penicillium, and the former feature is even more true with a rot caused by Sclerotinia.

When brown rot first appeared in the packing houses, search was made in the orchard to locate the origin of the trouble, with the result that even upon the tree affected lemons could be found. This was only the case during the wet season, which, in fact, is the only time when the rot is troublesome.

It is not the purpose of the present article to describe this trouble at length, but simply to place on record a description of the fungus and sufficient characterization of its effects to serve to identify this form of lemon decay. Lemons affected on the tree show a brownish, discolored area on the side or end, free from any mould or appearance of fungus, and without any decided softening of the rind, but gradually spreading and soon involving the whole lemon. The fruit keeps its size, shape, and solidity, even when totally affected, before which time it usually drops to the ground. The orchard occurrence is not generally abundant except in wet, warm spring weather or under like conditions. Affected lemons have a peculiar characteristic odor, and are readily identified by one familiar with the disease.

Lemons are usually picked quite green, washed in a machine consisting of a tank of water with revolving brushes, and then stored in boxes for several weeks to cure. At times of abundant prevalence of rot, great loss is experienced in such stored fruit. In lemons apparently sound when put away, affected spots develop on individuals here and there in the boxes. These are soon involved, and also all those which lie in contact with them. These again spread the trouble, and an extremely virulent decay results. Lemons affected in this way have the appearance above described, except that a rather delicate, white mycelium develops on the surface and grows from lemon to lemon, causing the contact infection. The trouble never spreads in the mass of stored fruit except by actual contact of the healthy lemon with an affected spot. When a large amount of fruit becomes affected the characteristic odor is very pronounced. Penicillium follows rapidly and covers the affected lemons.

With reference particularly to the cause of the trouble, the fungus, which comes out on affected fruit in moist air and spreads from lemon to lemon, consists of a sterile mycelium, composed of large branching, mostly continuous filaments. If an affected lemon be placed in water for several hours, this mycelium develops more richly upon the surface, forming a slimy, Saprolegnia-like growth. The fungus quickly reaches the fibrous core of the lemon, bits of which soaked in water are soon surrounded with a luxuriant growth

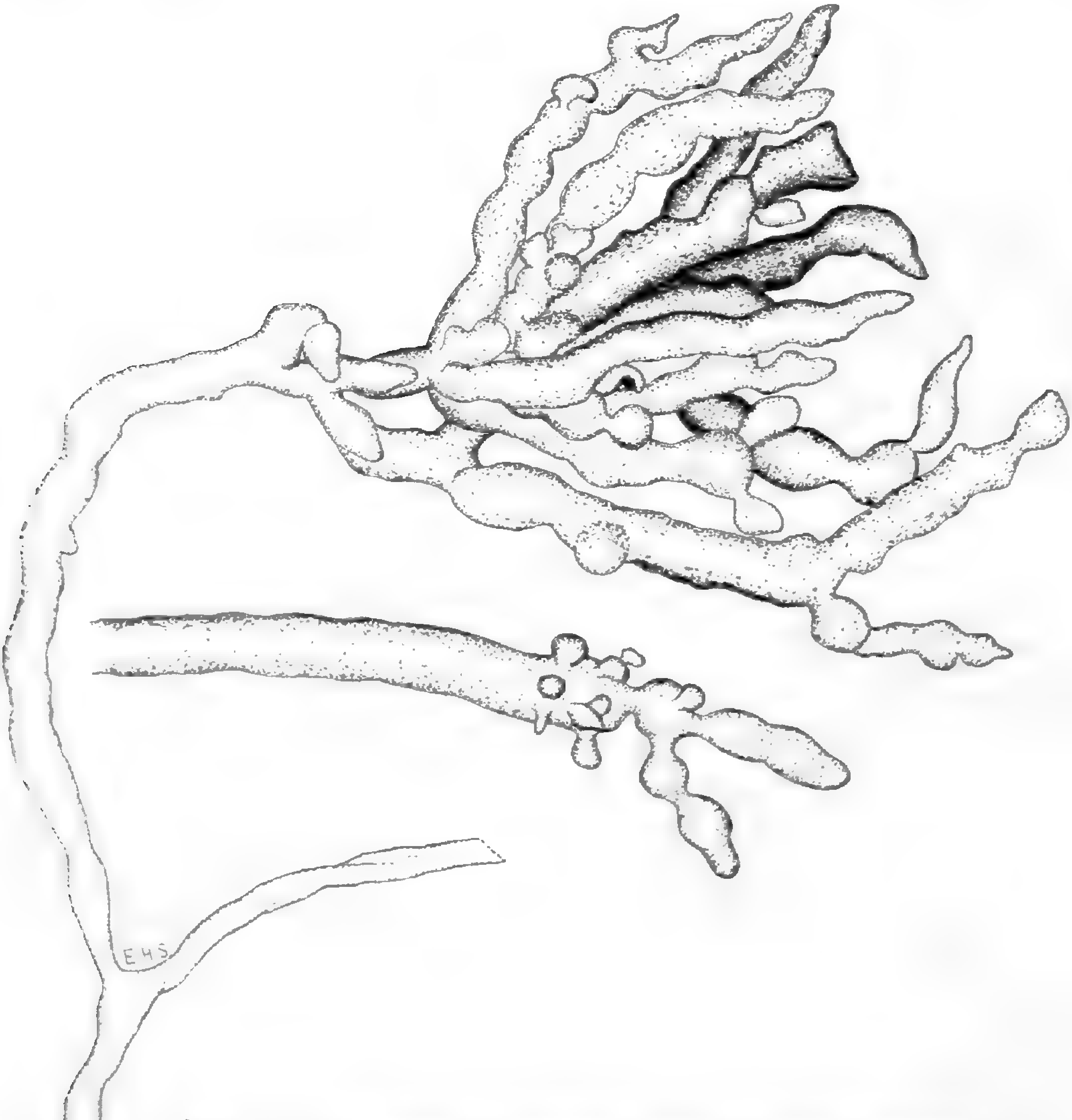

FIG. 1.—Sterile, aquatic mycelium, grown in dilute prune juice.

On dry or simply moist media (gelatin, bread, etc.) little or no growth can be obtained. In dilute prune juice the fungus grows with extreme vigor, forming a luxuriant mycelium of very large, branching, continuous filaments (*fig. 1*). Such growths are entirely sterile or nearly so. Occasionally there are produced a few large, ovate, terminal conidia or sporangia, of the phycomycete type, which germinate directly in water or form swarmspores. Numerous cultures in various liquid media have developed nothing but the mycelium and occasional spores of this kind. This fungus is nearly sterile under such conditions, and entirely so on affected lemons in the air, though with extreme vegetative vigor. Cultures of pieces of affected lemon in pure water, kept for a long time, usually develop nothing but mycelium, though occasionally conidia or sporangia are produced to some extent. Bits of this sterile mycelium placed on sound lemons in a moist chamber produce infection and characteristic rot. Lemons soaked in water, into

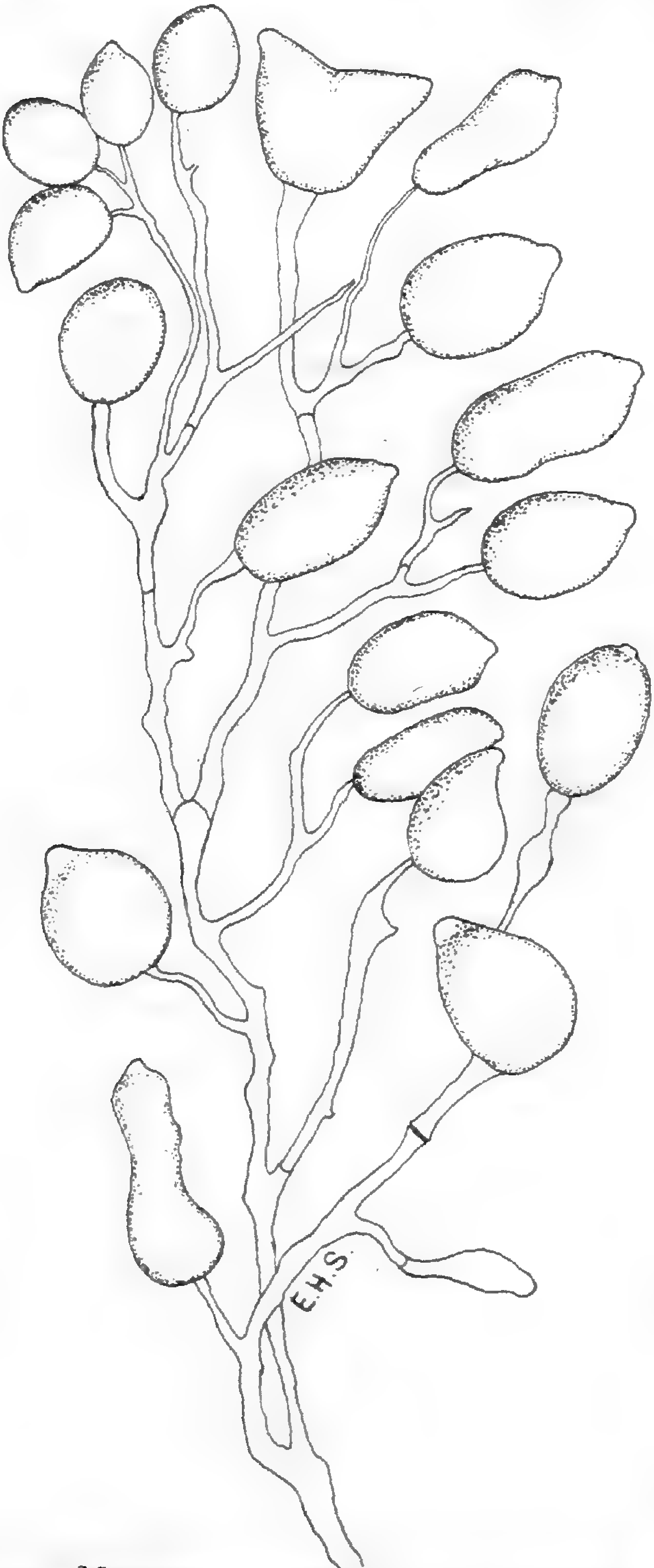

FIG. 2.—Mycelium with sporangia, from moist soil.

which a sterile culture of the fungus has been mixed, also become infected.

Affected lemons placed on moist soil (as in nature by falling from the tree) produce a visible mycelium upon the surface and make such ground highly infectious to sound fruit laid upon the surface. In soil thus inoculated the characteristic spore stage of the fungus has been found. This is also readily produced on wet filter paper in the bottom of a moist chamber containing an affected lemon. Upon an extremely delicate, fine, septate, branching mycelium, very numerous, terminal sporangia are produced (*fig. 2*), much as in Pythium under similar conditions. These sporangia differ, however, from those of the latter genus, in producing swarmspores by direct internal division, behaving in this respect like those of Phytophthora, which they also resemble in appearance (*fig. 3*). The appended description gives further details. These swarm-

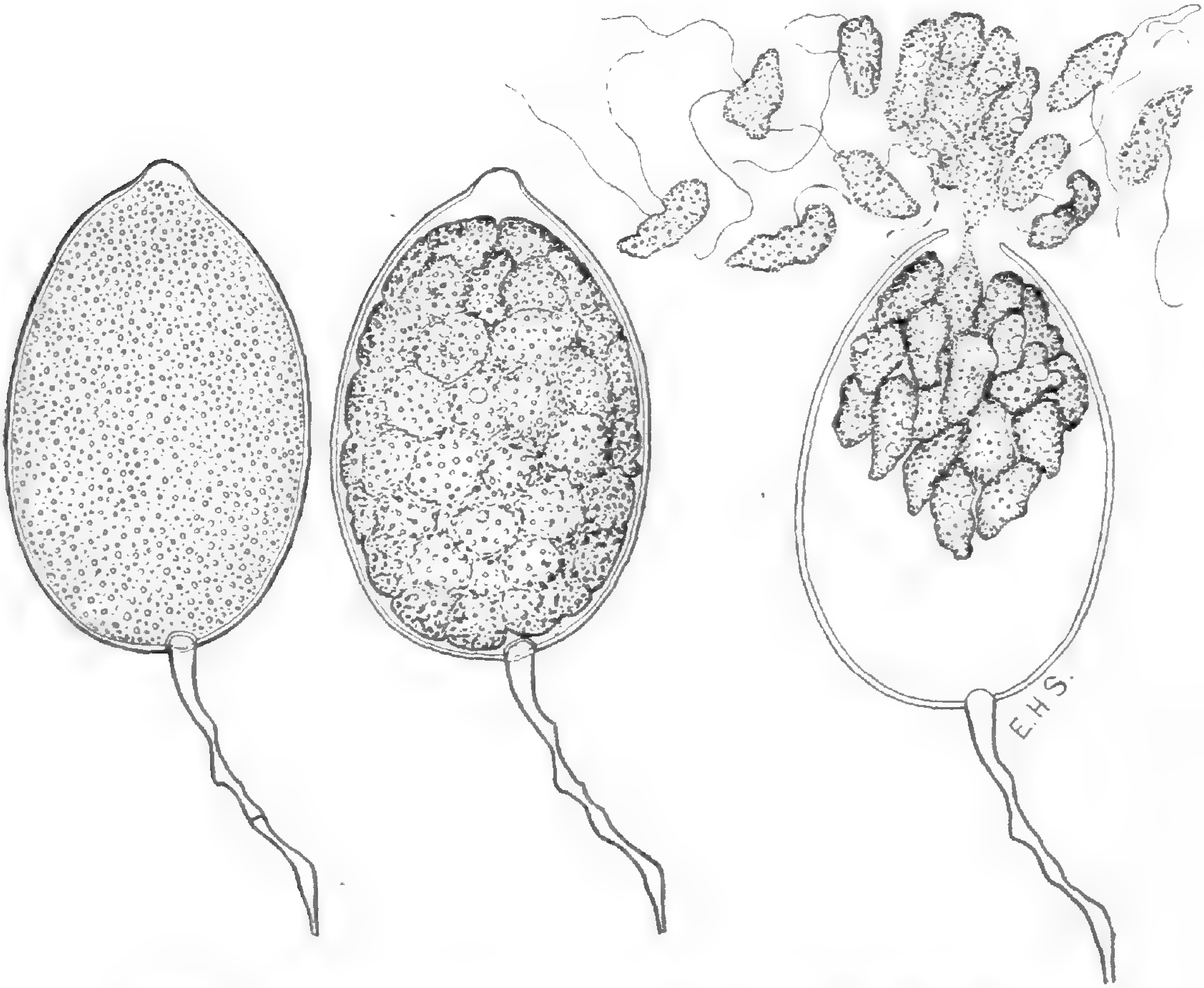

FIG. 3.—Stages in development of swarmspores from sporangia.

spores are extremely infectious to sound, green fruit in all stages of development.

Lemons on the tree become infected during the rainy winter and spring months, almost entirely on the lower part of the trees (which are allowed to branch close to the ground), and in the wettest part of the orchard. The fungus at all times shows a very decided moisture requirement for its development. Infection takes place by swarmspores from the soil, both on the tree and in the washing tank, in the latter case by the orchard dirt, dust, leaves, and other sediment which accumulates in the water.

The writers have given much consideration to the generic relations of this fungus, particularly as to whether it is sufficiently distinct from Pythium and from DE BARY's Pythiopsis. It is remarkable for the connection which it presents between the Phycomycetes of this nature. While similar to Pythium in habit, except as to its peculiar parasitism on the lemon, this species is definitely excluded from that genus by its internal formation of swarmspores. We have felt considerable hesitancy in separating this form from Pythiopsis, on account of the similarity in swarmspore formation; the latter, however, being founded on a species of such different habit, an entomophthorous form of the Saprolegnieae, and being practically unknown save from the original description, we feel justified in proposing a new genus for our species. It is particularly of interest as being more exactly intermediate between the Saprolegnieae and Peronosporeae than either Pythium or Pythiopsis, and also forming a close transition from Pythium to Phytophthora, having the swarmspore formation and something of the parasitic tendency of the latter. In brief, Pythiacystis has the soil habit of Pythium, the aquatic habit of the same and of the Saprolegnieae (including Pythiopsis) except for its usual sterility under such conditions, the sporangia formation of Pythium, the swarmspore formation of Pythiopsis and Phytophthora, and parasitic activity intermediate between Pythium and Phytophthora.

No indication of sexual reproduction has been observed in the large amount of material and numerous cultures examined.

An Experiment Station bulletin on the nature and control of this fungus will be issued in due time.

Pythiacystis Smith & Smith, n. gen.

Parasitic on living plants, or saprophytic with abundant moisture. Fertile mycelium delicate, septate, with numerous, terminal, sympodially developed sporangia. Aquatic mycelium typically sterile, with occasional conidia or sporangia. Filaments very large and vigorous, continuous, much branched.

Sporangia typically rounded or ovate, dividing internally into biciliate swarmspores which immediately become motile and emerge from a terminal opening.

Conidia similar to sporangia, germinating directly by a germ tube.

Sexual reproduction not observed.

Differs from Pythium in mode of swarmspore formation, and from Pythiopsis in habit. Closely intermediate between Saprolegnieae and Peronosporeae.

Pythiacystis citrophthora Smith & Smith, n. sp.—Parasitic on lemons, and occasionally other Citrus fruits, causing decay of green fruit on the tree and in the storehouse. Mycelium in affected fruit sterile, inhabiting rind and fibrous portions. Internal, except in moist air. Mycelium in water or nutrient liquids very vigorous, usually sterile, or occasionally with conidia or sporangia. Fruiting stage found typically in moist soil, in contact with affected fruit. Sporangia ovate or lemon-shaped, sometimes rounded, considerably elongated, or double, with terminal protuberance; $20\times30\mu$ to $60\times90\mu$, av. $35\times50\,\mu$. Produced in great abundance under favorable conditions. In water dividing quickly by internal division into 5 to 40 (usually about 30) swarmspores, which are immediately set free and discharged through a terminal pore.

Swarmspores 10 to 16 μ in diameter, at first elongated, becoming rounded; with two lateral cilia 30 to 40 μ in length. Actively motile when discharged, soon coming to rest and germinating.

Fungus abundant in winter and spring in southern California lemon orchards and packing houses, causing serious losses.

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CURRENT LITERATURE.

BOOK REVIEWS.

American fossil cycads.[1]

SINCE 1898 DR. WIELAND has been investigating the wonderful American display of fossil cycadean forms, usually referred to now as the Bennettitales. The investigation has demanded an unusual amount of patience and hard work in making the necessary collections and sections. The student of living plants has no adequate conception of the labor involved in obtaining valuable results from sectioning fossil material. The result of all this work now appears in a bulky memoir published by the Carnegie Institution. It is a veritable mine of information in reference to Bennettitales, a mine that will be worked by botanists for a long time to come. To present the results here would be to write another book. They are not essentially new, but they are so much more complete and more finely illustrated than ever before that the student of gymnosperms must always consult this volume.

The contents may be outlined by giving the chapter headings as follows: discoveries and collections, preservation and external characters, on the methods of section cutting, trunk structure, foliage, ovulate cones, bisporangiate axes, young fructifications, existing and fossil cycads compared, fern ancestry and angiosperm analogies.

The author is to be congratulated upon the amount of good work that he has accomplished and upon the fine and permanent form in which it has appeared. Morphologists can now lay hold of this material as they never could before, and organize it for general use.—J. M. C.

MINOR NOTICES.

Reproduction.—Under the title "multiplication and sexuality in plants," KÜSTER[2] has published some expanded lectures which were given in January and February of this year and constituted "an advance course for teachers." Vegetative multiplication is first considered in the higher plants, then in the lower. Sexual reproduction is treated historically, and then taken up from the standpoint of its evolution, the lower forms being treated first. The general problems discussed are: sexual affinity, hybridization, polyspermy, parthenogenesis, apogamy, apospory, and distribution of sexes. The book closes with remarks on theories of reproduction and sexuality. It is a convenient, compact, and reliable compendium of the subject.—CHARLES J. CHAMBERLAIN.

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[1] WIELAND, G. R., American fossil cycads. pp. 296. *pls. 50. figs. 138.* Carnegie Institution. 1906.

[2] KÜSTER, ERNST, Vermehrung und Sexualität bei den Pflanzen. 8vo. p. vi+120. *figs. 38.* Leipzig: B. C. Teubner. 1906. *M* 1.25.

Leaflets on Philippine botany.—Under this title A. D. E. ELMER proposes to issue in serial form articles on Philippine plants, both scientific and economic, printed in English, Latin, German, or French. This publication will appear at irregular intervals, at a subscription price of 1¾ cents per page, and may be obtained by addressing the editor at Manila. The first issue is a paper of 41 pages entitled *Philippine Rubiaceae*, by the editor, containing 150 species, of which 45 are new, representing 42 genera.—J. M. C.

Das Pflanzenreich.[3]—Part 26 contains the Droseraceae by L. DIELS. Drosophyllum, Dionaea, and Aldrovanda are regarded as monotypic genera; while Drosera is credited with 84 species, 5 of which are new. A very full discussion of structure and range precedes the synopsis.—J. M. C.

Pflanzenfamilien.[4]—Part 224 includes the completion of the Spiridentaceae, the Lepyrodontaceae, and the Pleurophascaceae, and a portion of the Neckeraceae, all by V. F. BROTHERUS. Part 225 continues the Ascolichenes by A. ZAHLBRUCKNER.—J. M. C.

NOTES FOR STUDENTS.

Revelations of the ultramicroscope.—GAIDUKOV has been seeing previously invisible things by means of SEIDENTOPF's ultramicroscope, and hastens to communicate them in two preliminary papers.[5] After mastering the rather difficult technique and the sources of error, he began by observing the expressed contents of a Vaucheria filament, but later found that it was possible to observe the contents *in situ*. He saw the ultramicroscopic particles of plasma and chlorophyll, the former white and blue, the latter red and green—colors whose significance is unknown as yet for lack of sufficient physical investigation of the instrument. He watched the collision of plasma particles with structureless oil drops and their recoil, and the like collisions of chlorophyll particles and their disappearance in the oil, in which the number of red and green chlorophyll granules steadily increased. This appears to be actually the formation of a colloidal solution of chlorophyll in oil—an oleosol.

In examining a living filament he found that the protoplasm occupied a much greater space than appears with ordinary illumination, only a very small part of the filament being optically empty. In the chloroplasts of Mesoçarpus, roundish or stellate flecks of chlorophyll particles are distributed through the stroma, whose structure is like that of the protoplasm; there is no indication of the solution of chlorophyll in oil droplets lying in the stroma—a widely accepted notion.

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[3] ENGLER, A., Das Pflanzenreich. 26 Heft. Droseraceae von L. DIELS. pp. 136. *figs. 40 (286), map 1.* Leipzig: Wilhelm Engelmann. 1906. *M* 6.80.

[4] ENGLER, A. und PRANTL, K., Die natürlichen Pflanzenfamilien. Lieferungen 224 and 225. Leipzig: Wilhelm Engelmann. 1906.

[5] GAIDUKOV, N., Untersuchungen mit Hilfe des Ultramikroskopes nach Seidentopf. Ber. Deutsch. Bot. Gesells. **24**: 107–112, 155–157. 1906.

The nucleus of Tradescantia appears to have a structure like protoplasm, but much more compact.

Bending movements of Oscillaria are accompanied by wave-like movements of particles in the cells; and the longitudinal movements by a streaming of particles on the surface in a direction opposite to that of the motion of the filament. These particles pass off into the water when they reach the end of the filament.

Ultramicroscopic organisms in figure-of-8 forms, and colonies in form like certain flagellates, similar to the organisms already described by RAEHLMANN, were found in every preparation.

Protoplasmic movements have been seen in all organisms investigated, and the ordinary rotation and streaming is by no means the simple flow it seems to be, but is probably initiated by a complex motion of the ultramicroscopic particles (ultramicrons) of the protoplasm, whose structure seems identical with that of colloidal solutions as determined by ZSIGMONDY with the instrument. The first movement, indeed, may be what has long been known as the Brownian movement, once so carefully distinguished from the "vital" ones as "purely physical."

In plasmolysis GAIDUKOV has seen the protoplasmic particles move from the periphery toward the center of the cell, changing shape at the same time from round to vermicular, while in the chloroplast simultaneously the vermicular chlorophyll particles creep out upon the surface. In Flagellatae there is a vigorous movement of particles in the region of the cilia and below the mouth opening, before the gross movements begin.

Whereas in chlorophyllose cells the cell wall is optically empty (*leer*), enabling one to see the cell contents clearly, the wall of bacteria and fungi has so complex a structure that nothing can be seen through it. Yet the purple bacteria which also work photosynthesis have a wall optically empty. These facts are believed to be related to the necessity for transparence to light in photosynthetic cells.—C. R. B.

Araucarieae.—A. C. SEWARD and SIBILLE O. FORD have published the results of a study of the Araucarieae.[6] The two living genera representing the group, Agathis and Araucaria, have long stood somewhat stiffly apart from other Coniferales, not only on account of the known facts in reference to them, but chiefly, perhaps, on account of lack of knowledge. The authors have marshalled our knowledge of extinct and living forms in this memoir; and however opinions may differ as to their conclusions, there can be only one opinion as to the value of the work. The subject is presented under the following captions: distribution, generic diagnosis, seedlings, stem anatomy, roots, leaves, leaf-traces, reproductive shoots, fossil Araucarieae, and phylogenetic considerations and conclusion. The details are too numerous to be included in a review, but the conclusions are too important to be passed over lightly.

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[6] SEWARD, A. C. and FORD, SIBILLE, O., The Araucarieae, recent and extinct Phil. Trans. Roy. Soc. London. B. **198**:305–411. *pls. 23–24. figs. 28.* 1906.

In general, the memoir is a contention that the recent brilliant work which has knit together cycads and Filicales has developed the too sweeping conclusion that all gymnosperms have the same phylogenetic connection; that the old view suggesting a connection between conifers and lycopods deserves more attention than it has been receiving; and that at least the Araucarieae strongly suggest a lycopod origin. It is urged upon paleobotanical evidence that the Araucarieae are the most primitive of Coniferales, certainly more primitive than the Abietineae; and that this testimony from history is supported by numerous evidences of relatively primitive structures still exhibited by Agathis and Araucaria. The difficult question of the Cordaitales, which seem to combine characters of Cycadales and Coniferales and so necessitate a common phylogeny, is disposed of by minimizing their resemblances to the latter, at least to the Araucarieae. It must be remarked that the authors repeatedly emphasize the fact that they are dealing only with the Araucarieae, and that it does not affect their main contention whether the other Coniferales are related to a filicinean ancestry through the Cordaitales or not. In developing the differences between the Araucarieae and other Coniferales, they have been so impressed by their importance that they have suggested a group *Araucariales*, coordinate with Coniferales, Cycadales, etc. For this group, at least, they claim a lycopod ancestry, through some such form as Lepidocarpon, emphasizing the seed-like sporangia recently described by SCOTT in that genus.

The authors are to be congratulated upon a very fair statement of their case, a statement which dodges none of the difficulties, and which really does not claim very much more than that an almost abandoned hypothesis must not be neglected.

A very interesting appendix to this memoir may be obtained by reading the report[7] of two recent meetings of the Linnean Society, at which various views as to the origin of gymnosperms were presented and combated by English students of the group.—J. M. C.

Items of taxonomic interest.—N. L. BRITTON (Bull. N. Y. Bot. Gard. **4**:115–127, 137–143. 1906) describes new species of Bahama plants under Coccolobis, Caesalpinia, Canavalia, Hibiscus, Heliotropium (2), Lantana (2), Cestrum, Stemmodontia, Anastraphia, Marsilea, Dondia, Cassia, Maytenus, Myroxylon, Opuntia, Limnanthemum, Metastelma, Aster.—W. H. BLANCHARD (Torreya **6**:147–149. 1906) has described 2 new species of Rubus (dewberries) from New England.—H. D. HOUSE (*idem* 150) has described a new Convolvulus from Georgia.—H. A. GLEASON (Bull. Torr. Bot. Club **33**:387–396. 1906) has revised the pedunculate species of Trillium, defining 19 species, 3 of which are new.—H. D. HOUSE (Rhodora **8**:117–122. 1906) has described the violets and violet hybrids of the District of Columbia and vicinity, recognizing 26 species, and describing 8 new hybrids.—M. L. FERNALD (*idem* 126–130) has described new species of Cyperus (2) and Eleocharis from Eastern North America.

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[7] New Phytol. **5**:68–76, 141–148. 1906.

—E. B. COPELAND (Philippine Jour. Sci. **1**: 143–166. *pls. 28.* 1906) has described 47 new species and 2 new genera (*Acrosorus* and *Thayeria*) of Philippine ferns.—SPENCER LE M. MOORE (Jour. Botany **44**: 217–224. 1906) has described 2 new genera of Acanthaceae from Madagascar, *Melittacanthus* and *Amphiestes*.—BUNZO HAYATA (Jour. Linn. Soc. Bot. **37**: 330. *pl. 16.* 1906) has described a new genus (*Taiwania*) of conifers from the Island of Formosa, belonging to the Taxodieae and nearest to Cunninghamia.—EDITH M. FARR (Ottawa Nat. **20**: 105–111. 1906) has described new species from the Canadian Rockies and Selkirks under Pachystima (4), Arnica, Hieracium, Dryas, and Ranunculus.—O. STAPF (Kew Bulletin 1906: 204) has published a new genus (*Diandrolyra*) of grasses whose native country is unknown.— O. E. JENNINGS (Annals Carnegie Mus. **3**: 480–485. 1906) has published new species under Kneiffia and Ibidium (Spiranthes) from Pennsylvania.—V. F. BROTHERUS (Hedwigia **45**: 271. 1906) has described a new genus (*Uleobryum*) of Pottiaceae from Peru.—F. LAMSON-SCRIBNER (Rhodora **8**: 137–146. 1906) has included in a newly named genus (*Sphenopholis*) the grasses that have been referred for many years to *Eatonia* Raf., recognizing 7 species.—W. H. BLANCHARD (*idem* 146–157) has described 5 new blackberries (Rubus) from Maine.—R. SCHLECHTER (Engler's Bot. Jahrb. **38**: 137–143. 1906) has described two new African genera (*Afrothismia* and *Oxygyne*) of Burmanniaceae.—J. C. ARTHUR and F. D. KERN (Bull. Torr. Bot. Club **33**: 403–438. 1906), in a revision of the N. Am. species of Peridermium, recognize 30 species, 10 of which are described as new.—K. K. MACKENZIE (*idem* 439–443) has described 4 new species of Carex.—LEROY ABRAMS (*idem* 445–446) has described 2 new southwestern species of Pentstemon.—J. M. C.

Japanese Experiment Station Bulletin.—A new departure in experiment station publications had been inaugurated by Professor HOZAI of the Imperial Central Agricultural Experiment Station of Tokio. In order to make the results of work carried on in the experiment stations of Japan accessible to investigators of other countries, a periodical Bulletin will be issued in which all work that may be of general interest will be published. The experimental system of Japan comprises 47 stations, whose work will in large part become available to the world through the publication of this Bulletin, printed partly in English and partly in German. The first number[8] contains 11 articles, some of which are briefly noted here to show the scope of the publication. S. MACHIDA reports on the influence of dilute solutions (0.3%) of Ca and Mg salts on the putrefactive action of bacteria. The rate of putrefaction was determined by the quantity of NH_3 formed in urine and in pepton solutions to which the salts had been added. It was found that the Ca-salts retard putrefaction, while Mg-salts favor the process.

Several articles of agronomic interest are given by G. DAIKUHARA on the correction of an unfavorable ratio of lime to magnesia, also on the lime factor

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[8] The Bulletin of the Imperial Central Agricultural Experiment Station, Japan. Vol. I. No. 1. pp. 94. *pls. 13.* Nishigahara, Tokio. December 1905.

for the tobacco plant, and on the application of magnesia in the form of magnesium sulfate for the rice plant. UYEDA gives an extended account of a new phytopathological bacterium (*Bacillus Nicotianae*) which produces a serious disease known as stem-rot and black-leg of tobacco. HORI gives an account of a smut on the cultivated bamboo. The fungus attacks the young internodes of growing branches, and as it may infect these at any time during the growing season, whole forests of bamboo often become infected. As the bamboo furnishes material for building as well as for household utensils and fences, the damage thus caused is considerable. The fungus is referred to *Ustilago Shiraiana* P. Henn.—H. HASSELBRING.

Respiratory enzymes.—PALLADIN announces his adherence to the theory of BACH and CHODAT, that normal respiration depends upon the presence of 1) oxidizable substance and 2) two enzymes, whose mixture was formerly designated oxidase, *a*) oxygenase, which has, attached to various radicals, the characteristic peroxid or hydroperoxid group O·O or O·OH and serves to transfer O_2, and *b*) peroxydase, which is a catalyser and renders active the oxygenase. When oxidative processes do not occur it is because one or two of the three are wanting. The less stable oxygenases, and those which with water quickly become hydroperoxids, are used up promptly, giving rise to some of the respiratory CO_2; so that often tests do not show any "oxidase" present in plant parts; but the peroxidases, which are very stable, can always be found.

From his researches PALLADIN concludes[9] that the prevalence of one or the other enzyme is connected with the stage of development of the plant. For anaerobic respiration prevails in embryonal organs and in lower plants, which alone are capable of anaerobic life. In the embryonal stage oxygenase is at a minimum, increasing with the passage into active life, and diminishing in organs which have ceased to grow.

Miss KRASNOSSELSKY,[10] working under PALLADIN's direction, finds in frozen onions and their sap no oxygenase, but peroxydases whose quantity increases with respiratory activity, if H_2O_2 be supplied, and continues to do so even when respiration falls. Katalase, however, is present in the sap after the freezing.

These researches are more and more justifying the opinion that the origin of "respiratory" CO_2 is very complex, and that more than one catalyser is taking part in the dissociation.—C. R. B.

Ancient history of ferns.—ARBER[11] has brought together the recent development of knowledge in reference to the history of ferns in a short paper that brings

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[9] PALLADIN, W., Bildung der verschiedenen Atmungsenzyme in Abhängigkeit von dem Entwicklungstadium des Pflanzen. Ber. Deutsch. Bot. Gesells. **24**:97–107. 1906.

[10] KRASNOSSELSKY, T., Bildung der Atmungsenzyme in verletzten Zwiebeln von *Allium Cepa*. Ber. Deutsch. Bot. Gesells. **24**:134–141. 1906.

[11] ARBER, E. A. NEWELL, On the past history of ferns. Annals of Botany **20**: 215–232. 1906.

the important facts well in view, however opinions may differ as to some of the conclusions. It is shown that the fern-like Cycadofilices, later called Pteridosperms, were a dominant group of the Carboniferous; but that the evidence for the existence of ferns in the modern sense is at present very uncertain. For any Carboniferous fern-like plants that may prove to be true ferns the author suggests the name *Primofilices*, since to distinguish among them definite eusporangiate and leptosporangiate habits is impossible. In fact, all the so-called "fructifications" of Paleozoic "marattiaceous ferns" may prove to be the microsporangiate structures of Pteridosperms. Until this is determined, the existence of eusporangiate ferns in the Paleozoic as a dominant group must remain uncertain. This also means that the old question as to whether the eusporangiate or the leptosporangiate type of ferns is the more primitive has lost its apparently sure answer from history. In fact, while the author gets sure evidence of leptosporangiate ferns in the Permian, he does not find similar satisfactory evidence of eusporangiate ferns until the Tertiary; although in both cases he recognizes the possible Paleozoic occurrence. As to the water ferns, the evidence of their existence does not become clear until the Tertiary. The claims for them in the Paleozoic are so much in conflict with all morphological testimony that they have never seemed to be very serious. The general conclusion in reference to the ferns seems to be that while Pteridosperms are a dominant group in the Paleozoic; and the Cycadophyta are one of the dominating groups of the Mesozoic; there is no evidence at present of the dominance of any fern group except that of the leptosporangiates in the Mesozoic and continuing into the present flora.—J. M. C.

Spores of Riccia glauca.—BEER[12] has investigated the development of the spores of *Riccia glauca*, contrasting his results with those of GARBER[13] on *R. natans*, and of LEWIS[14] on *R. crystallina*. The spore mother cells are at first separated by extremely delicate membranes in which no cellulose could be demonstrated, and upon them secondary and tertiary thickening layers are deposited which give pectose-cellulose reactions. The secondary layer becomes more or less mucilaginous, sometimes separating completely from the primary wall, at other times remaining partly adherent and becoming drawn out into strands bridging the space between the primary wall and the tertiary layer. No nutritive material was found between the isolated mother cells, and no non-nucleated reticular resting nucleus was found. The large deep-staining nucleolus consists of a number of deeply chromatic granules embedded in a faintly staining matrix. A long and well-marked spirem thread occurs in the prophase of the division of the mother cell. The reduced number of chromosomes is 7 or 8. In telo-

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[12] BEER, RUDOLF, On the development of the spores of *Riccia glauca*. Annals of Botany **20**:275–291. *pls. 21–22.* 1906.

[13] BOT. GAZETTE **37**:161–177. 1904.

[14] BOT. GAZETTE **41**:109–138. 1906.

phase a number of chromatic bodies (presumably derivatives of the chromosomes) are distributed on the linin fibers, and subsequently aggregate to form the lobular nucleolus of the resting nucleus. The first spore wall is cuticularized from a very early period, and within it, at the equatorial rim, a plug of mucilage is deposited. The second spore wall is formed within the first wall, and is also cuticularized; at first it appears homogeneous, but subseqently is composed of three regions. The endospore (pectose and cellulose) is formed late, and is often separated from the second wall by a thin band of dark material.—J. M. C.

Postelsia.[15]—Four years ago the first volume under this title appeared,[16] containing seven papers by members of the Minnesota Seaside Station on the coast of Vancouver. The present volume is printed in the same handsome style, and also contains seven papers as follows: Observations on plant distribution in Renfrew district of Vancouver Island (pp. 1–132. *pls. 1–11*), by C. O. ROSENDAHL; The Conifers of Vancouver Island (pp. 133–212. *pls. 12–15*), by F. K. BUTTERS; Hepaticae of Vancouver Island (pp. 213–235), by ALEXANDER W. EVANS; Some western Helvellineae (pp. 236–244), by D. S. HONE; *Renfrewia parvula*, a new kelp from Vancouver Island (pp. 245–274. *pls. 16–19*), by ROBERT F. GRIGGS; A study of the tide-pools on the west coast of Vancouver Island (pp. 275–304, *pls. 20–25*), by ISABEL HENKEL; Some geological features of the Minnesota Seaside Station (pp. 305–347. *pls. 26–33*), by C. W. HALL.

The paper on plant distribution reaches the conclusion that the pteridophytes are poor in species for so moist a region, that the gymnosperms constitute the great mass of the vegetation, and that the monocotyledons are more important than the dicotyledons. The paper on conifers contains very interesting observations, treats Picea, Tsuga, and Pseudotsuga as sections under Abies, and organizes a key to the northwestern genera on the basis of foliage. *Renfrewia* is a new genus of kelps nearest to Laminaria and Cymathere.—J. M. C.

Synapsis and reduction.—From a study of the pollen mother cells of *Acer platanoides*, *Salomonia biflora*, *Ginkgo biloba*, and *Botrychium obliquum* CARDIFF draws the following conclusions.[17] Synapsis is a constant morphological character of the mother cell, and the unilateral position of the synaptic knot is probably due to gravity. Previous to synapsis the chromatin is in two or more threads which arrange themselves in pairs, longitudinally, and finally fuse during synapsis, but there is not a complete mingling of chromatin substance in the chromatic thread. The thread splits longitudinally in the first mitosis, probably along the line of previous fusion. The chromosomes are of different sizes and do not behave alike at the first mitosis.

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[15] The year book of the Minnesota Seaside Station. 1906. pp. 364. *pls. 33.* Obtained from Josephine E. Tilden, Univ. Minn., Minneapolis. $2.25.

[16] BOT. GAZETTE **34**:468. 1902.

[17] CARDIFF, I. D., A study of reduction and synapsis. Bull. Torr. Bot. Club **33**:271–306. *pls. 12–15.* 1906.

It is probable that at fertilization there is a nuclear but not a chromatin fusion, and that the paternal and maternal chromatin retain their identity throughout the sporophytic phase, finally fusing, in so far as they fuse at all, during synapsis. If this be true, the two important phenomena of fertilization—stimulus to growth and intermingling of ancestral characters—are widely separated, the stimulus to growth occurring when the nuclei fuse, and the mingling of characters being delayed until synapsis.—CHARLES J. CHAMBERLAIN.

Nutrition of the gymnosperm egg.—Miss STOPES and FUJII[18] have been investigating the nutritive relations of the surrounding tissues to the egg in gymnosperms. As is well known, about the "central cell," and later about the egg, there is organized usually a very distinct jacket of nutritive cells, whose inner walls are conspicuously thickened and pitted. The authors find that the delicate walls of the endosperm cells are pitted in the same way; and that the large pits of the jacket cell-walls are closed by a membrane perforated only by plasmodesmen. This latter fact is the most interesting one of the paper, for it precludes the old notion of nuclear migration or of any transfer of solid material from the jacket cells to the egg. The jacket cells are regarded as glandular, secreting substances for the digestion of the starch and proteid granules stored in the endosperm. The statement is made in the summary that the jacket cells "are considered the phylogenetic homologues of the angiospermic antipodals," a statement evidently based upon their similar function.—J. M. C.

Ecological survey of Northern Michigan.—Under the direction of C. C. ADAMS there has been published[19] the report of an ecological survey conducted by the University Museum of the University of Michigan in 1904. The regions selected were Porcupine Mountains in Ontonagon County, on the south shore of Lake Superior, and Isle Royale, an island near the Canadian shore. Especially significant is the report by A. G. RUTHVEN on the relation of the plants and animals of these regions to their environment. Lines of survey were run across the region examined, in such a way as to include examples of all the representative habitats. These habitats were then examined in as much detail as time permitted, and special attention was given to the relations of the "biota" to its environment. In this study attention was directed particularly to the forces and conditions composing the environment, in order that the dominant forces might be clearly recognized. The results are too numerous and detailed for mention, but the work is unique and extremely suggestive.—J. M. C.

Ecology of algae.—FRITSCH[20] has made a statement of some of the problems

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[18] STOPES, M. C. and FUJII, K., The nutritive relations of the surrounding tissues to the archegonia in gymnosperms. Beih. Bot. Centralb. **20**:1–24. *pl. 1.* 1906.

[19] An ecological survey in Northern Michigan. Prepared under the direction of CHAS. C. ADAMS. Publ. in Rep. State Geol. Survey for 1905. pp. 133. *figs. 21.* 1906.

[20] FRITSCH, F. E., Problems in aquatic biology, with special reference to the study of algal periodicity. New Phytol. **5**:149–169. 1906.

connected with the study of algal ecology, and has suggested some means towards their solution. The first problem considered is the determination of what shall constitute a formation, and the contrast with terrestrial formations is made. Suggestions are made as to the significant unit and examples are given. Chief attention, however, is given to algal periodicity, the seasonal variations of algae being much greater than those of terrestrial plants. "In most cases in an aquatic flora a number of dominant forms succeed one another in the course of a year, and after their period of prevalence is past they disappear either suddenly or gradually." Periodicity of algae is either seasonal or irregular, and the factors concerned in both of these cases are discussed. In illustration of his statements, the author discusses the algal flora of a particular pond. The paper is a distinct stimulus to the study of pond life in an effective way.—J. M. C.

Decay of timber.—Following the lines of investigation laid down by HARTIG in his *Zersetzungserscheinungen des Holzes*, BULLER[21] has contributed a further study on the subject of the decay of timber caused by the higher fungi. The form studied is the common *Polyporus squamosus*, which is found on many species of broad-leaved trees. Like other forms of this class, the fungus gains entrance to the tree through wound surfaces. The mycelium progresses more rapidly in a longitudinal direction in the wood, so that the decayed region extends many feet up and down the trunk and principal branches, while advancing only a few inches in a radial direction. The hyphae penetrate into all the wood cells. The decaying wood is lighter in color than the sound wood. In the final stages of the decay the wood cracks into cuboidal blocks, with the intervening crevices filled with strands of the white mycelium of the fungus. The decayed wood is somewhat richer in carbon and poorer in oxygen and nitrogen than sound wood.—H. HASSELBRING.

Apogamy in Dasylirion.—WENT and BLAAUW[22] have described apogamy in *Dasylirion acrotrichum*, in the case of plants in cultivation in the Utrecht Botanical Garden. This Mexican species is dioecious, and no staminate plants exist in the garden, thus precluding the possibility of fertilization. A certain number of fruits matured sufficiently to attract attention, and an examination of the ovules discovered embryo sacs containing endosperm tissue in various stages of development, in some cases completely filling the sac. Dasylirion is thus added to the very few illustrations of endosperm-formation without fertilization. In these endosperm-containing sacs no embryos were found, but in some others a group of cells was discovered in the usual position of the egg-apparatus, which the authors seem justified, judging from the figures, in regarding as a young embryo. The position would suggest a case of parthenogenesis, but there is room for doubt, and the authors prefer to speak of it as a case of apogamy.—J. M. C.

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[21] BULLER, A. H. REGINALD, The biology of *Polyporus squamosus* Huds., a timber-destroying fungus. Jour. Econ. Biol. 1:101–138. *pls. 5–9.* 1906.

[22] WENT, F. E. F. C. and BLAAUW, A. H., A case of apogamy with *Dasylirion acrotrichum* Zucc. Recueil Trav. Bot. Néerland. no. 3. pp. 12. *pls. 5.* 1905.

Photosynthesis by carotin.—KOHL[23] shows by new experiments that the secondary maximum in the curve of photosynthesis, as drawn by ENGELMANN, is due to carotin. He eliminates the possible error in this determination (made by an improvement of the bacterial method), showing that the bacteria are in nowise affected by the F-rays alone. But when algae are illuminated only by rays absorbed by carotin, the movement of the bacteria begins, indicating evolution of O_2. He also shows that though O_2 is necessary to the formation of chlorophyll, etiolated leaves may become green in an O-free chamber, provided CO_2 is not in excess, since they can use the O_2 set free in photosynthesis. Of etiolin KOHL can find no trace, and he holds it certain that neither carotin nor xanthophyll (the latter probably a transformation product of the former) can be antecedents of chlorophyll. Whatever gives rise to it is probably colorless.—C. R. B.

Poisonous Colorado plants.—GLOVER[24] reports the results of studies of larkspur and other poisonous plants in Colorado. Of the eighteen species of Delphinium found in Colorado the most serious pests in this connection are *D. elongatum* and *D. Nelsonii*. He finds that the larkspur gradually becomes less and less toxic as it approaches the flowering period and finally becomes entirely harmless. The toxic principle has not yet been determined for these species, but is probably delphinine and some other related alkaloids. Other poisonous plants mentioned are species of Zygadenus, Cicuta, Lupinus, and Hymenoxys. The last plant is not strictly poisonous, but forms after being eaten a rubbery mass that may prove injurious. The bulletin contains a useful bibliography of the literature of plants poisonous to cattle on the range.—E. MEAD WILCOX.

Ecology in the Philippines.—It is a matter of no small interest to receive the first extended ecological study of a region of the Philippines. WHITFORD'S[25] account of the vegetation of the Lamao forest reserve introduces us to a tropical region, where the details of plant ecology are new and fascinating, and where the problems must be peculiarly complex. The Lamao forest reserve is in the province of Bataan (Luzon), on the east slope of a group of volcanic peaks known as Mount Mariveles. After the introductory statements as to geology and physiography, climate, and soil, the vegetation is discussed at length under six formations: Strand, Bambusa-Parkia, Anisoptera-Strombosia, Dipterocarpus-Shorea, Shorea-Plectronia, and Eugenia-Vaccinium. The half-tone plates are numerous and present most interesting views of tropical vegetation.—J. M. C.

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[23] KOHL, F. G., Die assimilatorische Funktion des Karotins. Ber. Deutsch. Bot. Gesells. **24**: 222–229. 1906.

[24] GLOVER, G. H., Larkspur and other poisonous plants. Bull. Col. Exp. Sta. **113**: 1–24. *pls. 1–8*. 1906.

[25] WHITFORD, H. N., The vegetation of the Lamao forest reserve. Philippine Jour. Sci. **1**: 373–431, 637–679. *map* and *pls. 1–45*. 1906.

Azotobacter.—STOKLASA and his assistants have been cultivating *Azotobacter chroococcum* and *Radiobacter* sp. to determine the fixation of nitrogen and the fermentative respiratory activity.[26] They do not confirm BEIJERINCK'S assertion that Radiobacter fixes free N, nor that Azotobacter in company therewith fixes more N than in pure culture. They conceive the fermentation of the mannits and of glucose by Azotobacter to be wrought by glycolytic enzymes which split them into lactic, acetic, and formic acids and alcohol. By the decomposition of these, CO_2 and H_2 are produced, the former at greater rate than in any organisms previously known. Thus 1^{gm} of Azotobacter, dry weight, produces on an average 1.3^{gm} CO_2 in 24 hours. The H_2 is believed to have an important rôle in the fixation of N.—C. R. B.

Subalpine scrub in New Zealand.—COCKAYNE[27] has named the distinct zone of plants on many New Zealand mountains between the limit of the forest and the subalpine meadow the "subalpine scrub." On Mount Fyffe this formation differs from the typical one in the paucity of species and in the great domination of *Cassinia albida*, a species peculiar to that locality, in places being almost a pure formation. *Ranunculus lobulatus*, another local species, is the principal plant beneath the scrub. Some of the shrubs are strongly xerophytic; and the author thinks that the amount of xerophylly observed in many New Zealand plants is by no means a measure of their adaptation to present environment, but rather a survival from previous more xerophytic conditions.—J. M. C.

Monoecism of Funaria hygrometrica.—BOODLE[28] has undertaken to settle the contradictory statements in reference to the distribution of the male and female organs of this species. It seems that bryological works describe it as monoecious; and that certain general textbooks speak of it as dioecious. It turns out that the bryologists are right, as might have been expected. "The male axis bears a terminal male flower, and produces a lateral branch (innovation) which forms a terminal female flower. The female branch may be inserted at different levels, sometimes high up, sometimes basally; it usually has a tuberous base bearing a tuft of rhizoids, and if torn away appears like an independent plant."—J. M. C.

Color of algae.—GAIDUKOV exposed the blue-green plates of Phormidium and the red Porphyra to the spectrum of a strong electric light.[29] In ten hours under all the green to violet rays the color had become yellow to brown-yellow,

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[26] STOKLASA, J., et al., Ueber die chemischen Vorgänge bei der Assimilation des elementaren Stickstoffes durch Azotobacter und Radiobacter. Ber. Deutsch. Bot. Gesells. **24**: 22–32. 1906.

[27] COCKAYNE, L., Notes on the subalpine scrub of Mount Fyffe. Trans. N. Z. Inst. **38**: 361–374. 1906.

[28] BOODLE, L. A., The monoecism of *Funaria hygrometrica* Sibth. Annals of Botany **20**: 293–299. 1906.

[29] GAIDUKOV, N., Die komplementäre chromatische Adaptation bei Porphyra und Phormidium. Ber. Deutsch. Bot. Gesells. **24**: 1–5. 1906.

remaining blue-green under the red to yellow rays. Porphyra remained red in the green–violet, but became green in the red–yellow. The pigments thus become of the complementary color to the incident light, and change in a time inversely proportional to the intensity of the light. The same change, but much slower, had been observed by the author in nature, and he considers this complementary chromatic adaptation the chief factor in determining the color of algae.—C. R. B.

Pollen tubes of Cucurbitaceae.—KIRKWOOD[30] has been studying the behavior of the pollen tubes of *Melothria pendula*, *Micrampelis lobata*, and *Cyclanthera explodens*. He has noted that the time elapsing between pollination and the arrival of the tube at the embryo sac in these species is 26, 19, and 41 hours respectively. The tubes pass chiefly over the surface of the conducting tissue, lining the stylar canal and covering the "placental lobes," and this is rich in starch. The suggestion is made that the tube is directed by "nutritive substances secreted by the conducting tissue," and that it "comes under the influence of a stronger stimulant emanating from the ovule," and "the source of this stimulus may be the endosperm nucleus."—J. M. C.

Morphology of Phyllocladus.—Miss ROBERTSON[31] has obtained some glimpses of Podocarpus from cultivated species and five collections of *P. alpinus* secured in New Zealand by Dr. COCKAYNE during 1902, 1903, and 1904. It is disappointing to learn that no critical stages were fixed, and that we are still on the outside of this interesting genus. However, it is of no small interest to learn that centripetal xylem occurs in the cladodes and is restricted to them. This feature is quite characteristic of the Taxus-forms; while the winged pollen grains belong to the Podocarpus-forms. These and other characters emphasize the intermediate position of Phyllocladus between the two prominent tribes of Taxaceae.—J. M. C.

Parichnos in recent plants.—HILL[32] has reached the conclusion that parichnos, a name given by BERTRAND to the strand of thin-walled parenchymatous tissue accompanying the leaf trace in a species of Lepidodendron, is represented among living species of Lycopodium and Isoetes by certain mucilage canals. The tissue to which the name was given is simply an early developmental stage of the canal. In recent plants parichnos is restricted chiefly to the sporophylls, as, for example, in *Isoetes Hystrix*, where two canals run longitudinally on each side of the sporangium, but do not extend into the cortex of the stem, as is the case in fossil forms.—J. M. C.

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[30] KIRKWOOD, JOSEPH EDWARD, The pollen tube in some of the Cucurbitaceae. Bull. Torr. Bot. Club **33**:327–342. *pls. 16–17*. 1906.

[31] ROBERTSON, AGNES, Some points in the morphology of *Phyllocladus alpinus* Hook. Annals of Botany **20**:259–265. *pls. 17–18*. 1906.

[32] HILL, T. G., On the presence of a parichnos in recent plants. Annals of Botany **20**:267–273. *pls. 19–20*. 1906.

Spore formation in Botrychium.—The development of the spores and the behavior of the tapetum in *Botrychium virginianum* are described by STEVENS.[33] CARDIFF had already published an essentially identical account of the tapetum.[34] STEVENS's term *tapetal plasmodium* seems to be a suggestive and convenient name for the peculiar tapetal mass as it appears in Botrychium and many other pteridophytes. The behavior of the kinoplasm and trophoplasm during the formation of spores from the mother cell indicates that these two plasms are interchangeable, each being able to become transformed into the other.—CHARLES J. CHAMBERLAIN.

Dichotomous leaves in Cycas.—SEWARD[35] has called attention to the dichotomous leaves of *C. Micholitzii,* a subterranean-stemmed species from Annam. Most of the pinnae are repeatedly dichotomous, but the terminal pinnae are simple and similar to those of other species of the genus. It seems that dichotomous pinnae in the cycads were first noted by MOORE in the Australian *Macrozamia heteromera.* The author suggests the possibility that the usual simple pinnate type of the cycadean leaf "may be the result of reduction from an older type characterized by the more primitive dichotomous habit."—J. M. C.

Diatomin.—KOHL was incited by the papers of MOLISCH[36] and TSWETT[37] to reinvestigate the coloring matter of diatoms,[38] having denied in his work on carotin the existence of a special pigment, "diatomin." He now finds that his conclusion was correct as regards any special "diatomin;" but the pigment is not carotin and xanthophyll alone, as he declared, chlorophyll, with the same absorption spectrum as in higher plants, being also present. The leucocyan of MOLISCH he does not find. The yellowish or brownish hue of the diatoms is due to the prevalence of carotin as compared with the higher plants.—C. R. B.

Germination in Ophioglossum.—The difficulty and the desirability of securing the germination of the spores of the pteriodophytes with tuberous gametophytes are well known. CAMPBELL announces (Annals Bot. **20:** 321) in a brief note that he has secured germination in certain Javanese species of Ophioglossum. In every case the characteristic endophytic fungus was present beyond the three-celled stage. In one case a gametophyte of thirteen cells was found; but no stage between this and mature gametophytes were secured.—J. M. C.

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[33] STEVENS, W. C., Spore formation in *Botrychium virginianum.* Annals of Bot. **19**:465–474. *pls. 18–20.* 1906.

[34] CARDIFF, I. D., The development of the sporangium of Botrychium. BOT. GAZETTE **39**:340–347. *pl. 9.* 1905.

[35] SEWARD, A. C., Notes on Cycads. Proc. Cambridge Phil. Soc. **13**:293–302. 1906.

[36] MOLISCH, H., Bot. Zeit. **63**^{1}:131–162. 1905.

[37] TSWETT, M., *ibid.* 273–278.

[38] KOHL, F. G., Die Farbstoffe der Diatomeen-Chromatophoren. Ber. Deutsch. Bot. Gesells. **24**:124–134. 1906.

Cytology of Entomophthoraceae.—One species of Empusa and four of Entomophthora have been studied by Riddle.[39] In Entomophthora the division is more or less typically mitotic. During prophase the chromosomes are formed by a direct aggregation of the chromatin granules without the previous formation of a spirem. In the formation of zygospores the fusing bodies are coenogametes. The writer suggests that the azygospore of Empusa is of the nature of a chlamydospore. Cytological conditions indicate that Entomophthora is a more highly developed genus than Empusa.—CHARLES J. CHAMBERLAIN.

Lime and sphagna.—As a result of cultures PAUL, in a preliminary paper,[40] confirms the older and still prevalent idea that the sphagna are very sensitive to the presence of $CaCO_3$ in the water in which they grow, and controverts the pronouncements of WEBER and of GRAEBNER. *Sphagnum rubellum* is most sensitive, bearing less than 77^{mg} $CaCO_3$ per liter (i. e., 0.0077%), while *S. recurvum,* least sensitive, bears less than 312^{mg}. *S. rubellum* changes its beautiful red to a blue, indicating an alkaline reaction, the more clearly the higher the lime content of the solution.—C. R. B.

Julianiaceae.—Under this name HEMSLEY[41] has established a new family of Mexican plants, known at present to contain two genera (Juliania and Orthopterygium) and five species. Its closest relationships are said to be with the Anacardiaceae and Cupuliferae; but the final judgment of the author places it in linear arrangement between Juglandaceae and Cupuliferae. "The absolute separation of the sexes and the very great diversity of the floral structure of the sexes, associated with pinnate leaves, offers a combination of characters probably without a parallel."—J. M. C.

Fossombronia.—HUMPHREY has described[42] in detail the germination of the spores and the development of the sex organs of a Californian species, *F. longiseta.* the first investigation of any member of the genus since LEITGEB'S, nearly 30 years ago. No striking anomalies appear. No centrosome was observed at any stage of nuclear division; blepharoplasts seem to appear *de novo,* and a *Nebenkörper* likewise, forming the middle piece of the sperm. The spermatids are of the pyramidal form described by IKENO in Marchantia, with no wall between the pair.—C. R. B.

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[39] RIDDLE, LINCOLN W., Contributions to the cytology of the Entomophthoraceae: preliminary communication. Rhodora **8**:67–68. 1906.

[40] PAUL, H., Zur Kalkfeindlichkeitsfrage der Torfmoose. Ber. Deutsch. Bot. Gesells. **24**:148–154. 1906.

[41] HEMSLEY, W. BOTTING, On the Julianiaceae, a new natural order of plants. Abstract. Read before Royal Society, London, June 28, 1906.

[42] HUMPHREY, H. B., The development of *Fossombronia longiseta* Aust. Annals of Botany **20**:83–108. *pls. 5–6.* 1906.

Anatomy of the Araliaceae.—VAN TIEGHEM[43] has published the results of a very extended anatomical study of the Araliaceae as a basis for their classification. He is convinced that he has discovered anatomical characters that are of great service in this way, and he applies them in establishing groups of genera, in making diagnoses of genera more precise, and in clearing up the positions of a number of critical species. The following six new genera are characterized: *Bonnierella, Mesopanax, Plerandropsis, Octotheca, Strobilopanax, Schizomeryta.*—J. M. C.

Germination among palms.—GATIN[44] has published an extended study of germination among palms, having included in his researches 58 species, representing 33 genera. The first and far the larger part of the paper deals with what are called "anatomical" studies, and one conclusion that is reached, among several others, is that the "cotyledon," so far as palms are concerned, is a single leaf and not a phylogenetic coalescence of two leaves. The second part deals with the chemistry of germination.—J. M. C.

Water relations of the coconut.—The anatomy of the root and leaf of this palm, as well as the conditions affecting the entrance and passage of water through the plant, have been investigated by COPELAND.[45] Maximum transpiration is found to favor maximum yield of fruit. Wind and intense sunlight accelerate transpiration. The roots should be abundantly supplied with water, though an excess is injurious. Irrigation is altogether practical.—RAYMOND H. POND.

Fossil roots of Sequoia.—LIGNIER[46] has identified the roots called *Radiculites reticulatus* as those of Sequoia, or of some allied form as Taxodium. The material studied is from the Stephanian of Grand' Croix, and its distinguishing feature is the reticulated cortical parenchyma. Comparing it with roots of similar structure in living plants, the conclusion is reached that it most nearly resembles the structure observed in the root of *Sequoia gigantea.*—J. M. C.

N. Am. Vernonieae.—GLEASON[47] has published a revision of the North American species of Vernonieae. Seventeen genera are characterized, two of which (*Eremosis* and *Orthopappus*) are new. The species number 143, of which 28 are new. The large genus is Vernonia, with 99 species, 25 of which are new; and the new genus Eremosis includes 15 species, 13 of which have heretofore been assigned usually to Vernonia.—J. M. C.

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[43] VAN TIEGHEM, PH., Recherches anatomiques sur la classification des Araliacées. Ann. Sci. Nat. Bot. IX. **4**:1–208. *figs. 54.* 1906.

[44] GATIN, C., Recherches sur la germination des palmiers. Ann. Sci. Nat. Bot. IX. **3**:191–315. *pls. 11. figs. 58.* 1906.

[45] COPELAND, E. B., On the water relations of the coconut palm. Philippine Jour. Sci. **1**: 6–57. *pls. 3.* 1906.

[46] LIGNIER, O., *Radiculites reticulatus*, radicelle fossile de Séquoinée. Bull. Soc. Bot. France IV. **6**:193–201. *figs. 5.* 1906.

[47] GLEASON, H. A., A revision of the North American Vernonieae. Bull. N. Y. Bot. Gard. **4**:144–243. 1906.

Apical meristems of monocotyl roots.—DAISY G. SCOTT[48] has investigated the root tips of Alisma, Butomus, Vallisneria, Ruppia, Zostera, Naias, Stratiotes, and Limnocharis. Her results support DE BARY'S statement in reference to the roots of monocotyledons in general, namely that there are three distinct groups of initials, one giving rise to calyptrogen, another to dermatogen and periblem, and the third to plerome.—J. M. C.

Megaspores of Lepidostrobus.—Mrs. D. H. SCOTT[49] has found that certain megaspores referred to KIDSTON'S Triletes belong to *Lepidostrobus foliaceus*, heretofore regarded as homosporous. They are peculiar in bearing a conspicuous appendage, said to be suggestive of the so-called "swimming apparatus" of Azolla. Many of these spores were found, and they are spoken of as "fairly common objects."—J. M. C.

N. Am. Hydnaceae.—BANKER[50] has published a revision of the pileate forms of Hydnaceae found in North America north of Panama, and including the adjacent islands. A few resupinate forms are included, but in general they are excluded, awaiting an examination of the Berkeley types. Ten genera are presented, two of them being new (*Leaia* and *Grandinioides*), and of the 63 species 10 are new.—J. M. C.

Fossil germinating spores.—SCOTT[51] has announced the discovery of germinating spores in a sporangium of *Stauropteris Oldhamia*. The discovery is important, for it has been in doubt whether this species should be regarded as a fern or a pteridosperm. The germination is distinctly fern-like, and confirms the anatomical resemblance of this species to the Botryopterideae.—J. M. C.

Apple scab.—LAWRENCE[52] reports further studies of the apple scab in Washington. In a comparative test of the relative effects of the dust spray mixture and the ordinary liquid Bordeaux it was found that the liquid was twelve times as effective as the dust spray. This is in accord with the results secured by CRANDALL[53] in Illinois.—E. MEAD WILCOX.

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[48] SCOTT, DAISY G., The apical meristems of the roots of certain aquatic monocotyledons. New Phytol. **5**: 119–129. *pl. 9.* 1906.

[49] SCOTT, RINA, On the megaspore of *Lepidostrobus foliaceus*. New Phytol. **5**: 116–19. *pl. 8. figs. 24–25.* 1906.

[50] BANKER, H. J., A contribution to a revision of the North American Hydnaceae. Mem. Torr. Bot. Club **12**: 99–194. 1906.

[51] SCOTT, D. H., The occurrence of germinating spores in *Stauropteris Oldhamia*. New Phytol. **5**: 170–172. 1906.

[52] LAWRENCE, W. H., Apple scab in Eastern Washington. Bull. Wash. Exp. Sta. **75**: 1–14. 1906.

[53] CRANDALL, C. S., Spraying apples. Relative merits of liquid and dust applications. Bull. Ill. Exp. Sta. **106**: 205–242. *pls. 1–9. figs. 1–5.* 1906. Review in BOT. GAZETTE **42**: 157. 1906.

NEWS.

Dr. H. A. Gleason has been appointed instructor in botany in the University of Illinois.

F. S. Earle has retired from the directorship of the Estación Agronómica Central de Cuba.

Dr. A. A. Lawson, Stanford University, has been advanced to an assistant professorship in botany.

C. B. Clarke, the well-known English systematist, died at Kew August 25, at the age of seventy-four years.

Dr. J. N. Rose, United States National Museum, left August 1 for his sixth collecting trip in Mexico, being especially interested in the Cacti.

Professor Charles Flahaut, Montpellier, has been elected an honorary member of the Zoological and Botanical Society of Vienna.—Science.

Mr. John G. Hall, Harvard University, has been appointed assistant in plant pathology in the North Carolina Agricultural Experiment Station.

During 1904 the additions to the Kew Herbarium were as follows: 8000 sheets presented by ninety persons and institutions; 4000 sheets purchased.

Professor C. R. Barnes, Dr. C. J. Chamberlain, and Dr. W. J. G. Land, University of Chicago, have spent the month of September in botanical work in Mexico.

Dr. H. C. Cowles, University of Chicago, will spend the autumn and early winter in Florida, studying the everglades under a grant from the Carnegie Institution.

Dr. A. F. Blakeslee has been appointed instructor in cryptogamic botany in Harvard University for the ensuing year, and will also give instruction in Radcliffe College. He has recently returned from two years study at Naples and Halle.

In commemoration of the twenty-fifth anniversary of its foundation, September 1907, the German Botanical Society proposes to publish a *Festschrift* of about 300 pages and 20 plates; and distinguished specialists, whether members or not, are asked to offer MSS. before January 1, 1907, to the Secretary, Professor Dr. C. Müller.

The death of H. Marshall Ward, professor of botany at Cambridge University, is announced as having occurred August 26. He succeeded Professor C. C. Babington at Cambridge in 1895, and died at the age of fifty-two years. His work on plant diseases is well known, and the splendid new botanical building, which was the result of his tireless activity, had only been occupied for two years.

THE *Beihefte zum Botanischen Centralblatt*, heretofore published by GEORG THIEME in Leipzig, will be published, beginning with the twentieth volume, by C. HEINRICH of Dresden. It will continue under the same editors, Drs. OSCAR UHLWORM of Berlin and F. G. KOHL of Marburg, and with the same two sections. The indefinite size of the parts enables the editors to promise publication with the utmost promptness.

THE COMMITTEE on "Applied Botany" of the International Association of Botanists met in Paris August 25–27, fourteen members being present. In addition to the customary addresses, it was decided to appoint a botanist to make a tour of the world to investigate and report upon the "resources of applied botany," the report to be made at the general meeting of the Association in 1908. It was estimated that 20,000 francs would be needed for this purpose, and the selection of a suitably trained botanist was left in the hands of a committee. It was decided to raise the money from various governments and public establishments. A committee was also appointed to investigate the invasions of plant diseases and to attempt to secure international legislation in reference to them.

A TIMELY MOVEMENT has been started in New Zealand to preserve the "Riccarton Bush." This fact is of great interest to botanists in general, for this "Bush" is the only remaining portion of a vast forest that once covered the region, and is the last piece of forest of its kind in the world. It is near the city of Christchurch, and a list of its species shows a combination of rare plants that exists in no other place. The dominant tree is *Podocarpus dacrydioides*, and other large trees are *P. totarra*, *P. spicatus*, *Elaeocarpus dentatus*, and *E. Hookerianus*. If this forest were destroyed, it would be a distinct loss to botanical science, which for years to come will need the material it can supply. The government of New Zealand has voted £1500 toward its acquisition, and there is still some £5000 to raise. It is to be hoped that nothing will interfere with the success of this movement. Those interested in it may communicate with Dr. L. COCKAYNE, Ollivier's Road, Christchurch, N. Z.

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OCTOBER, 1906

THE DEVELOPMENT OF AGARICUS CAMPESTRIS.*

GEO. F. ATKINSON.

(WITH PLATES VII–XII)

IN some respects the history of the study of the Hymeniales does not present the same progress which can be seen in the other groups of fungi, or indeed in nearly all other groups of plants. The earliest period, that of the study and classification of species and genera, presents in the main the same aspects which have been characteristic of the early study of all plants; but the progress made up to the present time is not in proportion to the time and energy expended, due to certain difficulties, some inherent in the nature of the plants themselves, and others due to the lack of an adequate knowledge of their anatomy and development.

The second period, that of the study of the morphology and development, began more than half a century ago. It is true that in the early part of the 19th century, nearly a century ago, quite an elaborate theory of the development of the Hymeniales, especially the Agaricaceae, was evolved by NEES VON ESENBECK.[1] But his theory, embellished as it is with his philosophical ideas of the evolution and metamorphosis of these plants from the puffballs and truffles; in which he was evidently influenced by the philosophy expressed in the *Vorwort* of GOETHE'S *Farbenlehre*, that in a book dealing with

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* Contribution from the Department of Botany of Cornell University. No. 110. Paper presented before Section G, of the A. A. A. S., at the New Orleans meeting.

[1] Das System der Pilze und Schwämme, ein Versuch von Dr. C. O. NEES VON ESENBECK, I–XXXVI, 1–329, 44 plates, Würzburg, 1816. See also NEES VON ESENBECK, Plantarum Mycetoidarum in Hort. Bonn. obs. evolutio. Nov. Act. Natur. Curios. **16**: pars 1. 1832, for development of *Agaricus volvaceus*.

natural phenomena the writer should make use of a lively imagination in order to make it real to the reader; and especially because there is such lack of definiteness as to the forms studied, though it is quite evident he refers more especially to species of Amanita, presents little that is helpful to the present discussion.

At that early period it was an important forward step to show, as DUTROCHET[2] did in 1834, that the large fungi were only the fruit bodies of the plants then known as "Byssus," which spread usually underground or in the substance of organic bodies; and for TROG[3] in 1837 to recognize the two different parts in the life history, the vegetative stage or mycelium and the fruiting stage or carpophore, and that this is the product of germinating spores; though MICHELI had stated as early as 1729[4] that the fruit bodies of some fungi did not come immediately from the seed (spores), but the seeds first produce a large root which grows for several years in the ground, and then gives rise to the fruit body (referring to *Polyporus tuberaster*). But during the early and middle portion of the 19th century the work on the morphology and anatomy of these plants, and the descriptions and illustrations of species, was far in advance of the work on development and the organization of the parts of the fruit body. Unfortunately the study of the morphology and development of the Hymeniales has not kept pace with the same studies in other groups of plants. J. SCHMITZ[5] studied the very early stages of five different species. While the work appears to be very carefully done for that early time, it does not meet modern requirements; and while his results perhaps in the main are not far out of the way for the species studied (*Cantharellus sinuosus*, *C. tubaeformis*, *Cortinarius bulliardi* (Pers.) Fr., *Coprinus niveus*, *Hydnum imbricatum*), it will be seen later he was led into a mistake in formulating a general law, based on these five species, to apply to the development of all the pileate fungi.

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[2] Mém. **2**:173. 1834.

[3] Ueber das Wachsthum der Schwämme, Flora **20**:609. 1837.

[4] Nova plantarum genera 134. 1729.

[5] Mycologische Beobachtungen, als Beiträge zur Lebens- und Entwickelungsgeschichte einiger Schwämme aus der Klasse der Gastromyceten und Hymenomyceten. Linnaea **16**:141–215. *pls. 6–7.* 1842. See especially the part II, Ueber die Bildung neuer Theile bei den Hymenomyceten, vorzugsweise den Pileaten. Idem 168–179.

BONORDEN[6] deals briefly with the anatomical structure of the genera recognized by FRIES in his *Epicrisis*. He does not discuss the differentiation of the parts in the young fruit body, but describes somewhat in detail the different forms of the universal veil, its mode of dehiscence, and its relation to the partial veil and the pileus in certain species of Lepiota (pp. 178–181). He says, very briefly (p. 8): "From the mycelium rises the fruit body of the fungus (stroma, thallus), either naked from the first or enclosed in an envelop (velum, volva). The latter consists always of very much elongated cells, tubes, which are like the tissue of the mycelium, and has therefore always a structure very different from that of the fruit body of the fungus; it is to be regarded as a continuation of the mycelium. The envelop is ruptured by the further growth of the pileus and is thrown off, but sometimes remains a part of the same and forms the epidermis of the pileus, on which account this is so different in structure in the case of the gastromycetes and pileated fungi from the other parts of the fungus."

H. HOFFMAN contributed at that time some important work on the anatomy and morphology, and as early as 1856 gave a very brief account of the origin of the hymenium of *Agaricus campestris.*[7] In speaking of his studies of the developmental history of the lamellae in very different types (*l. c.*, p. 145) he cites three extremes: *Agaricus carneo-tomentosus* (*Panus torulosus*), where they arise at the apex of the young fruit body; *Agaricus campestris*, where they originate deeper in the interior and develop laterally; and *Hymenogaster klotzschii*, where they remain concealed in the interior of the fungus. In describing the development of *Agaricus campestris* (p. 145) he says (I give a free translation): "It begins, as BULLIARD has already very well represented (Champ. d. France. *pl. 514, fig. L.* 1791–1809), in the form of small spheres which for a part rest upon thick mycelium strands. This stroma is formed as in the former case [*Agaricus carneo-tomentosus*, the stroma of which, he says, at first quite homogeneous, is formed out of felted filamentous cells]. Gradually the same takes on an elongate form; the interior cells grow in a perpen-

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[6] Handbuch der Allgemeine Mycologie 147–196. 1851.

[7] Pollinarien und Spermatien bei Agaricus. Bot. Zeit. **14**: 137–148, 153–163. *pl.* 5. 1856.

dicular direction, the upper ones grow laterally, and then bend abruptly downward; the ends of these cells abjoint a parenchyma which forms the beginning of the lamellae; the under surface of these young lamellae is somewhat even and has no longer any connection with the stroma tissue lying close beneath, which later sinks down as a ring. The hymenial layer opens here round about at the side."

A few years later[8] he describes the development of a number of additional forms, all of which were gymnocarp except one, *Marasmius oreades*, and he remarks (p. 401) that this peculiarity of the internal origin of the hymenium is characteristic of many other Agaricaceae, as was shown in his larger work[9] which appeared in the following year.

The work of HOFFMANN was followed by DEBARY'S[10] study of the development of several species of Agaricaceae and Gastromycetes, by HARTIG'S study of *Agaricus melleus*,[11] by BREFELD'S studies on species of Coprinus,[12] and by the incomplete study of a large number of Agaricaceae by FAYOD[13] nearly twenty years ago, which was the last serious attempt (which I have as yet seen) at a study of the development of the Agaricaceae. Even these few studies do not agree in the account of development which they give of the same or related species. Furthermore, they are very incomplete and unsatisfactory, owing either to the methods employed (freehand sections by the earlier students), or in the scanty material at hand, which did not provide sufficient numbers of the early stages of development or a sufficiently full series of stages.

The difficulties in method are now overcome, but the other difficulties, those of obtaining sufficient material in all stages of development, are still serious in the great number of species. This is because

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[8] HERMANN HOFFMANN, Beiträge zur Entwickelungsgeschichte und Anatomie der Agaricineen. Bot. Zeit. **18**:389–395, 397–404. *pls. 13–14.* 1860.

[9] Icones Analyticae Fungorum, Abbildungen und Beschreibungen von Pilzer mit besonderer Rücksicht auf Anatomie und Entwickelungsgeschichte 1–105. *pls. 1–24.* 1861.

[10] Morphologie und Physiologie der Pilze, Flechten und Myxomyceten 68. 1866.

[11] Wichtige Krankheiten der Waldbäume, etc. 25. 1874.

[12] Unters. a. d. Gesammtgebiet d. Mycol. **3**:13–122. *pls. 1–9.* 1877.

[13] Prodrome d'une histoire naturelle des Agaricinées. Ann. Sci. Nat. Bot. VII. **9**:181–411. *pls. 6–7.* 1889.

of the fact that at present few species have been cultivated artificially (except in the genus Coprinus by BREFELD, *l. c.*) so as to obtain the stages of development, and because the feral species nearly all pass their early and critical stages of development within the substratum and therefore are difficult to find, and at the same time it is often difficult to be certain to what species they appertain. These difficulties have probably played an important part in discouraging the further study of development of the Agaricaceae.

It is rather surprising, however, that even in the present time we do not have a sufficiently clear, full, and accurate account of the development of the fruit body of *Agaricus campestris*, especially the origin and differentiation of the various parts of the plant. This is the more so because this species is so common and of such wide distribution, but especially because it has been cultivated for so many years under conditions in which large numbers of carpophores in all conceivable stages of development are so easily obtained. Perhaps the very commonness and richness of the material has been the chief reason of its having been passed by.

Having given some attention to the study of the Agaricaceae for several years, especially as to their economic and biologic significance, as well as to the recognition of species and genera, the need of studies of development has been brought very forcibly to my attention, and I have been obtaining material for this study in several different genera. The meager and conflicting accounts which we have of the development of *Agaricus campestris*, as well as the ease with which material can be obtained, has led me to deal with this species first.

DEBARY[14] says the fruit body of many Agaricaceae (*Agaricus campestris*, *A. praecox*, *Coprinus micaceus* and relatives) is in its early youth a body interwoven out of delicate, dense, and uniform hyphae. At a very early stage, through differentiation of the original homogeneous weft, the principal parts of the fruit body are outlined and limited. On the interior of the upper part of the body a small and narrow air space of the form of a horizontal ring arises through the separation of the tissue elements. The portion which lies above becomes the pileus, the tissue present surrounded by it and below it

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[14] Morphologie und Physiologie der Pilze, Flechten und Myxomyceten 68. 1866. Leipzig.

becomes the stem. The tissue on the outside of it corresponds to the edge of the pileus, but its hyphae continue without interruption or change into the outer surface of the stem below.

In 1874 R. HARTIG,[15] in his study of the development of *Agaricus melleus*, says that "the investigation of the earliest condition of the fruit body of *Agaricus melleus* shows that here, as well as in the Agaricaceae not provided with a veil, the pileus arises through a superficial annular furrow which in the beginning is completely open to the outside, and that later through growth of the marginal hyphae of the pileus and of the stem the annular furrow becomes covered over with a hyphal layer, the veil." He further says that if one compares his *fig. 20* (which shows the veil covering the hymenial tract) with DEBARY'S *fig. 26* (*l. c.*) of the young *Agaricus campestris*, "it appears from the agreement of the two figures that the conjecture is justified that also by this last fruit body in the region of the hymenial tract a subsequent growing together of the hyphae of the pileus and stem has taken place." Longitudinal sections of the young fruit body of *Agaricus campestris* at this stage do give the suggestion that the veil originates as HARTIG described for *Agaricus melleus*. DEBARY evidently did not study the very young stages of *Agaricus campestris*, for all his figures of longitudinal sections show the veil covering the hymenial area. It seems that without reinvestigating the question he adopted HARTIG'S suggestion that the development in *Agaricus campestris* followed the same course as that described by HARTIG for *Agaricus melleus*. In his later work[16] he says in reference to those forms with a "marginal veil" (*velum partiale* of FRIES): "Up to the first formation of the pileus on the summit of the stipe-primordium the phenomena are the same in essential points as in the gymnocarpous forms" (referring to his figures of *Collybia dryophila*, p. 55). "The young pileus is entirely delimited from the stipe by a transverse annular furrow running along its future hymenial surface. But then the superficial hyphal layers of the stipe and of the young pileus send out numerous branches toward one another from the edges of the furrow; these unite into

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[15] Wichtige Krankheiten der Waldbäume, etc. 25. *pl. 106.* 1874.

[16] Comparative morphology and biology of the fungi, etc. 289–290. 1887. English edition.

a close weft, the marginal veil, which bridges over the furrow and closes it on the outside" (referring to figure of *Agaricus melleus* copied from HARTIG). To be certain that DEBARY here refers also to *Agaricus campestris* I quote also from page 291: "Most marginal veils are formed in the same way as that of *Agaricus melleus*, and *fig. 132* of *A. campestris* will serve to illustrate these remarks." *Fig. 132* is reproduced from his original work in 1866. In addition, on page 295 he says: "The account given above of the development of the species which are furnished with a marginal veil is founded, wherever it departs from my former statements, chiefly upon the facts discovered by HARTIG and BREFELD;" and on page 297, after discussing the different types of development in the Agaricaceae and his former statements, he says: "So far as these statements related to Coprinus they have been shown by BREFELD'S researches to be incorrect; my own did not pay sufficient regard to the earliest stages of development. I will not even maintain that they are quite correct for *Agaricus campestris*, ... but readily allow that the facts in the case are always the same as in *A. melleus*, and that the first extension of the marginal veil over the hymenial surface which was originally exposed had there also been overlooked."

GOEBEL[17] says: "These veil-formations are connected with the entire growth of the fructification; the species with a naked pileus are by their nature gymnocarpous." In speaking of the young fructifications of *Agaricus campestris*, he says: "These are at first pear-shaped bodies composed of young uniform hyphae, and each of these bodies is a rudimentary stipe, from the upper part of which the pileus will be developed. At an early period the hyphal tissue gives way in such a manner as to form an annular air cavity beneath the summit of the stalk, this cavity enlarges with the growth of the whole body, its upper wall forming the under side of the pileus, from which the radial hymenial lamellae grow in downward direction and fill up the cavity." His account thus supports DEBARY'S earlier account, but the evidence presented in illustrations is not sufficiently convincing in view of the controverted nature of the question and especially in view of the fact that gross anatomy and freehand sections

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[17] Outlines of classification and special morphology of plants 132–134. 1887. English edition.

do not show the early stages of organization and differentiation, and Goebel's figures (*fig. 89, l. c.*) of the section of the young fruit bodies are made after the young pileus is differentiated from the stipe. No evidence is given that this text book account is the result of original investigation, and it is more likely that Goebel here is relying on the early account given by DeBary, and the still earlier one given by Hoffmann cited above.

In a similar way, in describing the early stages of development of *Agaricus campestris*,[18] I have followed DeBary's later account as follows (p. 7): "At the same time a veil is formed over the gills by threads which grow from the stem upward to the side of the button, and from the side of the button down toward the stem to meet them. This covers up the gills at an early period." Aside from the extensive work of Fayod in 1889,[19] little work seems to have been done on the development of the young sporocarps of the Agaricaceae since the publication of DeBary's work in 1887.

In January 1905 an excellent opportunity presented itself for obtaining material in the required stages of development. Cultures had been made in boxes in the greenhouse of the commercial variety of *Agaricus campestris* known as Columbia, sold by the Pure Culture Spawn Company of Missouri. In many cases large numbers of young carpophores were formed at the surface of the substratum which were clean and in excellent condition for study. Preliminary examinations were made by freehand sections, and by staining in order to determine the age and size of the fruit bodies which should be prepared. In fruit bodies about 1^{mm} in diameter there was no evidence of a superficial annular furrow nor of any internal differentiation. Fruit bodies, therefore, from 1^{mm} to 4^{mm} were selected, fixed in chromo-acetic acid, imbedded in paraffin, microtomed, and stained, some in acid fuchsin and some in methyl blue.

The youngest stage is the primordium of the carpophore, a homogeneous body composed of slender uniform dense hyphae, intricately interwoven, and surrounded by a very thin layer of hyphae of a

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[18] Studies in American fungi, mushrooms, edible, poisonous, etc., 1st edition, Ithaca, N. Y., 1900; 2d ed. 1901; and New York 1903.

[19] Prodrome d'une histoire naturelle des Agaricinées. Ann. Sci. Nat. Bot. VII. **9**:181–411. *pls. 6–7.* 1889.

looser and less dense arrangement. This layer is the "universal veil." It is quite distinct in the young stages of these cultivated varieties, continues to increase in extent until the parts of the fruit body are differentiated and the young pileus and stem are manifest by external differences in form. Then it ceases to grow and is torn apart into white floccose patches on the pileus, as will be seen later. In the very young primordia then there is no evidence of a differentiation into stem and pileus in any of the many individuals which I have examined. As the primordia become slightly larger and older, but still before there is any evidence on the outside of an annular furrow or of any differentiation into pileus and stipe, longitudinal sections which are stained show two small deeply stained internal areas near the upper end of the young fruit body and some distance in from the surface. The hyphae here are not yet differentiated, but are richer in protoplasm, showing the origin of a new and special center of growth. This area is an annular one within the fruit body. Very soon afterward this area increases somewhat in extent and many hyphae begin to grow from the upper portion of this area downward. This is the primordial layer of the hymenium. It first arises when the tissue of the fruit body is homogeneous and compact except for the loose thin envelop. The hyphae which grow downward at this early stage are quite characteristic. They are slender and terete, tapering out into a long slender point. This enables them to pierce between the other hyphae of the compact fruit body. In fact at this time there are similar hyphae in the more central and upper portions, where the stem and pileus are to be differentiated, but in no other place at this time is there a definite center of growth which indicates the organization of any special part. These hyphae, partly at least, provide for intercalary growth of the young fruit body. Soon after the hyphae in the primordial layer of the hymenium begin to grow downward, there is a cessation of growth just below this area which results in the rupture and separation of the hyphae at this point in a corresponding internal annular area, forming the well known "gill cavity," which at first is very minute.

This annular primordium of the hymenium marks the differentiation of the primordium of the fruit body into the primordium of the pileus and that of the stem and veil, the latter being the tissue of the young fruit body external to the hymenial primordium and continuous with what is to be the margin of the pileus above and with the undifferentiated stem surface below. The downward growing hyphae now take on a different form. They are still slender, but are even and blunt and are very densely crowded side by side, are very rich in protoplasm compared with the hyphae of the rest of the young carpophore and consequently take a deep stain.

This first growth takes place on the under side of the young pileus primordium. The vegetative activity in this region of the young pileus is very great, and is very soon extended outward on the periphery or margin of the young pileus, as shown by the very rapid radial growth of the hyphae at the margin of the pileus, but still some distance in from the surface. This radial growth is also accompanied by a very strong hyponastic growth, so that the threads curve downward, and soon it is so strong that the margin of the pileus is strongly incurved, the hyponastic growth appearing to be stronger at the margin and near it than further inward.

At the same time the primordium of the marginal veil increases by intercalary growth. In the participation of the hyphae at the margin of the pileus in the formation of the veil, they seem to show a greater activity in growth so far as the density of the growth and richness in protoplasm is concerned; while the larger portion toward the stem, also increasing by intercalary growth, becomes looser by the rapid elongation of its elements and their partial separation, thus forming numerous small air spaces. This seems to have an important bearing on the supply of fresh air to the young forming hymenium where the air spaces become continually larger, and the first air space formed underneath the annular primordium of the hymenium not only gives place for the development of the latter but also provides aeration. Thus while the veil serves the purpose of protection to the young hymenium, its structure is such as to provide aeration also. After the differentiation of the hymenial primordium, the lateral growth of the pileus is accentuated so that it becomes broader than the stem portion, and now is formed the external annular furrow. Very soon after the hymenial primordium is organized, the tissue of the pileus primordium, or end of the fruit body, takes on a deeper stain in an area extending inward and some depth below the surface, showing that the pileus primordium is becoming definitely organized through the central portion (*fig. 4*), also sometimes seen in freehand sections in older stages as a compact area (*fig. 15*).

In the very early stage of the hymenial primordium the under surface is even, but very soon the outlines of the gills begin to form by the more rapid downward growth in radial lines. Very soon after the young gills begin to form, the surface of the stem is differentiated. This occurs in such a way as to show that the surface of the stem portion of the young fruit body does not become the surface of the stem except at its extreme lower portion, which probably corresponds to the bulb even when a bulb is not manifest as a thicker portion of the stem. From a point at the junction of the original annular primordium of the hymenium, or the junction of the young stem with the pileus at the inner end of the gills, and then extending obliquely downward and outward, the hyphae take on more active intercalary growth and a richer content of protoplasm. This marks the origin of the cortex of the stem, and distinguishes it very sharply from the elements of the veil and from the internal tissue of the stem which is to be the medulla by a deeper color in stained preparations; also in fresh freehand sections it is usually very clearly seen with the unaided eye as a whitish more compact area which shows well in ordinary photographs at this stage.

This study shows very clearly that the hymenium in *Agaricus campestris* is endogeneous in its origin, as HOFFMANN described so early as 1856 (*l. c.*), and that DEBARY'S first account of the development of this species in 1866 was correct so far as it went; but he did not succeed in obtaining for study carpophores sufficiently young to enable him to speak with certainty after HARTIG had thrown doubt on his conclusions as a result of his study of *Agaricus melleus.*

Not only is the hymenium endogenous in its origin, but the differentiation of the stipe and pileus is simultaneous; that is, the initial stages of the stipe and pileus as distinct structures are organized and made evident in longitudinal sections by the origin of the hymenial primordium. In all the sections that I have examined of this species at this stage, there is no evidence of differentiation of the pileus from the stem before the earliest evidence of the hymenial primordium. We should not conclude, however, this mode of development is necessarily to be found in other plants until they have been studied, though it is probable that it is true for at least some of the other species of Agaricus (Psalliota). FAYOD found that usually the primordium of the pileus was organized in the apex of the homogeneous young carpophore before the appearance of the primordium of the hymenium, and this seems to be true in certain species of Hypholoma studied by one of my students. In fact FAYOD asserts that this can be accepted as a general law. The primordium of the pileus is the first to appear in the organization of the parts of the carpophore from its primordium. It is shown by the area of hyphae composing it taking on a deeper stain in sections. It is in the form of an inverted bowl convex above, concave below, and *Agaricus rubellus* (*Psalliota rubella*) is one of the forms which he studied. The only exceptions which he admits are the coriaceous forms like Lentinus (*l. c.*, p. 296). In this respect these cultivated forms of *Agaricus campestris* show also an exception to this rule, and the primordium of the pileus is to be regarded as diffuse in the primordium of the carpophore, as he suggests for the coriaceous forms.

The question of the simultaneous organization of the pileus and stipe from a young homogeneous fruit body is an interesting one in view of the different theories held by some of the earlier students. Thus FRIES[20] said: "Omnia organa simul, nulla subevolutione nova successive explicantur. Omnes extremitates ipsius Fungi explicati jam in aetate juvenili adsunt," *i. e.*, "all organs are unfolded simultaneously, none by new successive development. All parts (or extremities) of the unfolded fungus itself are already present in the young stage." He thus believed that in the very young fruit body the organs or parts, though rudimentary and invisible, were all present, their manifestation and expression was a matter of unfolding.

This interesting conception is shown also in another place (*l. c.* 40), where he expresses his view of the general mode of growth of the fungi as compared with that of the algae as follows: "Fungi in omnes plerumque directiones a centro, quod junius, sese expandunt," *i. e.*, "Fungi, though young, expand from the center in almost all directions." All the parts being present, the growth in the center pushed them outward, as they enlarged, into their respective positions, while

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[20] E. FRIES, Systema orbis vegetabilis, part 1, 40, 43.

the growth in the case of the algae was at the periphery—"explicantur ita, ut extremitates semper sint juniores" (*l. c.* 53).

Then as to the relative time, or priority of the shaping of the different parts, FRIES says (*l. c.* 44): "Pileus v. c. in Agarico formatus est prius quam stipes pronascitur. Stipes enim pilei, cum quo contiguus, prolongatio et receptaculi pars," *i. e.*, "the pileus, for example, in Agaricus is formed before the stipe is produced. The stipe certainly is a prolongation of the pileus with which it is contiguous, and part of the receptacle."

J. SCHMITZ[21] in his *Mycologische Beobachtungen*, as a result of the study of several forms, holds an entirely different view. He agrees that according to his own observations in many cases all parts of the fungus are formed and present in a very young stage. But he cannot understand, nor believe, that these parts are formed at once, that is, simultaneously with the origin of the fruit body as if by the touch of a fairy wand ("wie durch einen Zauberschlag," p. 174). That at certain young stages all parts are to be considered present and yet invisible he regards as belonging to the domain of pure speculation, a hypothesis suited to a philosophical mode of representation or idealization, and not corresponding to reality. SCHMITZ gives an account of his studies on *Cantharellus sinuosus*, *C. tubaeformis*, *Agaricus bulliardi* Pers. (=*Cortinarius bulliardi* [Pers.] Fr.), *Coprinus niveus*, and *Hydnum repandum*, and believes he is justified in formulating for the pileate fungi a law of development as follows: "1st, that a successive formation of single parts or organs takes place; 2d, that this appearance of new parts rises upward just as gradually as in the case of the higher plants, in such a way that the higher standing parts naturally come to view later than the lower parts, that the matrix or hypothallus appears before the stipe, the stipe before the pileus, and the pileus before the hymenium.[22] In *Agaricus* (*Crepidotus*) *variabilis*

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[21] Ueber die Bildung neuer Theile bei den Hymenomyceten, vorzugsweise den Pileaten. Linnaea **16**:168–179. 1842.

[22] "Ich glaube also, dass man bei der Pileaten als Gesetz aufstellen darf, dass 1) eine successive Bildung der einzelen Theile oder Organe vor sich gehe; 2) dass dieses Hervortreten der neuen Theile ebenso graduell aufwärts steige, wie bei den höhern Pflanzen, so nämlich, dass die höherstehenden wesentlichen später als die untern zum Vorschein kommen, also die Matrix vor dem Stipes, dieser vor dem Pileus und der letztere (an und für sich) vor dem Hymenium auftrete."

OERSTED[23] says that the stem is produced first, and afterward the pileus.

In the forms of *Agaricus campestris* studied here, as I have shown, the young homogeneous fruit body (*figs. 1, 2*) shows no differentiation into parts (except the rudimentary universal veil), and it is to be considered as the primordium of the carpophore. It is not a stem, nor is it a pileus, there is no differentiation to show even the rudiments or primordia of stem or pileus; there is no more active growth manifest in one place than in another, and no separate group of hyphae with richer protoplasmic content which gives a differential stain. It cannot therefore be considered as a rudimentary stem, as GOEBEL (*l. c.* 132–138) has suggested. It is true we might speak of a stem end and a pileus end, but the application of these terms to the portions of the carpophore primordium which are later to be organized into pileus and stem primordia does not predicate their existence before organization takes place. But soon the differentiation takes place by the appearance of the primordium of the hymenium, which at once delimits also the primordia of pileus, stipe, and marginal veil (*figs. 3–5*). This condition answers well to the conception of FRIES that all parts are present in the young stage, though he conceived them to be present in the still younger stages, which we find is not the case.

DECANDOLLE[24] says that in the case of Agaricus the upper part or pileus develops before the lower part, or stipe. Without critical study of the very young stages one might be led to this conclusion by an examination of certain large pileate short-stemmed forms, and perhaps DECANDOLLE examined such plants. According to FAYOD (*l. c.* 279–280) the pileus is differentiated first, the hymenium

[23] OERSTED, A. S.: Iagttagelser anstillede i Löbet af Vinteren 1863–64, som have ledet til Opdagelsen af de hidtil ukjendte Befrugtningsorganer hos Blapsvampene.—Oversigt over det Kongelige danske Videnskabernes Selskabs Forhandlinger, p. 11. *pls. 1–2.* 1865. Copenhagen.

See translation, Observations made in the course of the winter of 1863–64, which have led to the discovery of the hitherto unknown organs of fructification in the Agarici by A. S. OERSTED. Quart. Jour. Microscop. Sci. **8**: 18–26. 1868.

[24] "Dans plusieurs, tels que les Agarics, la partie supérieure, qu'on nomme le chapeau, paraît développée avant l'inférieure, qu'on a comparée à une tige ou à un pédoncle; l'inverse semble avoir lieu dans les Clavaires qui paraissent croître de bas en haut." Organographie végétale **1**: 384. 1827.

and stipe later, and it is interesting to note that W. G. SMITH[25] in his study of *Coprinus radiatus* says that the cells of the pileus and the hairs which form the veil are the first to appear (*l. c.* 62), but his study does not seem to have been exact, and a comparison of such a form as Coprinus with Agaricus (Psalliota) is not pertinent at present except as it bears on the attempt of some to formulate a general law of growth.

If we now turn to the law formulated by SCHMITZ for the order of succession of the different parts of the pileate fungi, we see that *Agaricus campestris* does not conform to it, but that it is more in accordance with the idea expressed in the first sentence quoted from FRIES, that all parts of the fungus unfold simultaneously. This must not, however, be taken wholly to support FRIES' conception of the young sporocarp nor his idea of central growth. While it is likely that a number of other fungi will be found to agree with *Agaricus campestris* in the mode of organization of the parts of the plant from the primordium of the sporocarp, it is certain that no law of organization and succession of the parts can be formulated which will hold good of all the pileate fungi. There are probably some, as suggested above, in which the pileus and stipe primordia are organized before the primordium of the hymenium, and many others probably in which the stem is partially or quite well organized before there is even a primordium of the pileus, in which case the development would be in conformity with SCHMITZ's law given above. This is very likely the case with certain long, slender-stemmed species of Marasmius, of such plants as *Polyporus lucidus* Leys. (*Ganoderma lucida*), and others. But we must wait until the different types have been carefully studied from the very young stages in microtome sections.

FAYOD (*l. c.*), who studied a large number of Agaricaceae, formulates the general law that the pileus is organized first within the young primordium as a pileogenous layer (*couche piléogène*), which arises by internal differentiation, marked by the more rapid growth of the hyphal elements and their richer content in protoplasm. This layer is in the form of a shallow inverted bowl, convex above, concave below. This is surrounded on the sides and above by a thin layer

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[25] Reproduction in *Coprinus radiatus*. Grevillea **4**:53–65. *pls.* 54–61. 1875.

which he calls the primordial cuticle (*cuticle primordiale*). From his description the primordial cuticle varies in character and probably in structure also, and it is difficult to accept his conception of a primordial cuticle as a homologous structure in the large series of forms to which he applies the term. For example, he recognizes three main types in the development of the Agaricaceae: 1st, the gymnocarpous forms; 2d, the angiocarpous forms; 3d, the endocarpous forms, and the primordial cuticle is present in all except in a very few of the gymnocarpous forms. In the gymnocarpous forms the primordial cuticle consists generally of a more dense layer of tissue underneath which the pileogenous layer is formed. The margin of this becomes the border of the pileus, and as it extends laterally it dislocates at this point the primordial cuticle, so that the primordium of the hymenium which now arises is of exogenous origin, thus giving rise to the gymnocarpous type. Examples are *Panus stipticus*, *Cantharellus cibarius*, *Marasmius rotula*, *Collybia racemosa*, etc. Thus while DEBARY believed the pileus in the gymnocarpous forms originated exogenously, FAYOD holds that it originates endogenously; but in discussing farther certain other forms he admits that the pileus is formed in the manner indicated by DEBARY, and he states that the discussion which he has raised here is more in regard to a principle than fact, and he would not have raised the question at all had it not been for the fact that his study of the angiocarpous forms had shown him the importance of the pileogenous layer.

In many of the angiocarpous forms the primordial cuticle would seem from his own description to be a different structure from what it is in the gymnocarpous forms, for he says: "The hyphae which emanate from the pileogenous layer do not reach the surface of the primordium. As a consequence the primordial cuticle, which acquires here a very considerable thickness, preserves its integrity and continues to increase up to the time of the formation of the lamellae and stipe, that is, up to the second period of development." Here he recognizes the primordial cuticle as identical with the universal veil, and he would call it general veil (*voile général*), although it is often formed in some cases by parts also of the subjacent tissue of the primordium, were it not for the fact that he wishes to place it in the same category as the non-integral element of the primordium in the gymnocarpous forms which he considers a primordial cuticle.

The angiocarpous forms he further divides into two types, subangiocarpous and angiocarpous. In the subangiocarpous type the universal veil (*cuticule primordiale*), being continuous over the pileus and stem, forms the veil which is known as the "partial veil" or "marginal veil" of authors. He says (p. 286) it is probably characteristic of Flammula, Inocybe, Dermocybe, Hygrocybe, Psalliota, Lepiota, Psathyrella, Coprinus, and most of the Tricholomae. In the true angiocarpous types there is a cuticle of the pileus which is organized underneath the primordial cuticle or universal veil, so that at maturity the universal veil separates and forms floccose patches, or a volva, or may disappear by gelatinization. As examples he cites Agrocybe (*Pholiota praecox*, *Naucoria semiorbicularis*, etc.), Pholiotina (*Pholiota blattaria*, *P. togularis*, etc.), *Rozites* Karsten (*Pholiota caperata*), *Nemataloma* Karsten, some species of Panaeolus, Telamonia, and probably Locellina and Chitonia; the volva in the last three genera he considers to be only a very thick universal veil.

In the endocarpous forms the primordium of the fruit body is differentiated on the interior of a primitive bulb which he calls the primordial bulb (*bulbe primordial*), to which belong the greater number of species of Amanita, Volvaria, and some species of Phlegmacium. Since this type does not concern us here it will not be in place to discuss it.

From the foregoing it is seen that FAYOD places Psalliota (which includes *Agaricus campestris*) in his type of subangiocarpous forms. Among these forms he studied *Agaricus rubellus* Gillet (*Psalliota rubella*). While he does not describe the development of this species (his discussions of development are in the form of general conclusions), he says that it belongs to the subangiocarpous type, and his *fig. 4, pl. 7*, shows the primordial cuticle to consist of rather loose radiating threads connected on the sides where it extends down over the lamellae and stipe with the thicker portion covering the stem. Although FAYOD placed *Agaricus campestris* also in his subangiocarpous type, a study of these cultivated forms shows that it would belong to his true angiocarpous type because of the free universal veil entirely independent of the marginal veil, the universal veil eventually separating into floccose patches on the surface of the pileus as in *Rozites caperata* (Pers.) Karsten (*Pholiota caperata* Pers.).

During the later period of growth and the beginning of elongation of the plant, the marginal veil increases in thickness and extent. It is entirely free from the lamellae, the hymenial cavity being quite distinct from the first and becoming greater by the expansion of the pileus and marginal veil, and also by the elongation of the portion of the stem above its attachment. The increase in the surface extent of the marginal veil is considerable and results in throwing the upper surface into radiate folds which are quite noticeable, especially in the well developed individuals. In the young primordium at the time of the organization of the parts of the carpophore the marginal veil is attached over a large part of the outer surface of the stem primordium, the lower end, perhaps that portion which corresponds to the bulb in other species, being free. It thus remains attached over the stem surface for a considerable period during growth. As the period of elongation advances, the veil begins to separate from the stem at the lower end and is gradually torn off and upward as the pileus expands and the stem elongates. The tension of the connecting fibers can very easily be seen between the stem and the under surface of the veil, and is well shown in *fig. 20*. It therefore forms a sheath over the stem except a short section of the lower end, and the portion above the marginal veil which is elongating. This sheath is loosened from below upward except at the upper point at attachment to the stem. The outer margin of the veil is attached to the rounded and thick margin of the pileus, and being of considerable thickness in these cultivated forms the lower edge of the veil is separated first from the outer surface of the pileus margin (*fig. 40*), and the inner upper edge is separated last from the inner surface of the pileus margin. The margin of the veil is therefore furrowed (*figs. 18, 19*). A thick marginal veil of this type is called a "double veil," a type which is very characteristic of certain other species of Agaricus where it is more highly developed, especially in *Agaricus arvensis*, where the lower portion of the veil splits radially. It is very striking in *Agaricus rodmani* Pk., where the forking of the veil extends almost to the stem.[26] In *Agaricus placomyces* Pk. the veil is often similar to

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[26] See *fig. 17*, ATKINSON, Studies of American fungi, mushrooms, edible, poisonous, etc. 1900, 1901, Ithaca; 1903, New York.

that of *Agaricus arvensis* (*figs. 21, 22* in Studies Am. fungi, etc.), while in *Agaricus silvicola* and others the lower half of the marginal veil is often separated into patches (*l. c. fig. 20*). In the pasture or field forms of *Agaricus campestris* the marginal veil is thinner, but even here its double character is often manifest (*fig. 7, l. c.*).

The growth of the pileus which at first is strongly hyponastic becomes less so as the pileus expands. The upper surface gradually ceases to grow and the extension of the underlying part often tears the pileus cuticle into fibrous scales. The growth of the pileus gradually becomes epinastic, as the lower area and the hymenophore with the gills now grow more rapidly than the middle and upper portions. This causes the pileus to become plane, or in old specimens the margin itself becomes upturned. This peculiarity in the growth of the Agaricaceae during the period of elongation was supposed by some of the earlier botanists[27] to be due to the influence of light, for it was thought by them to be necessary that the hymenium should be turned up to the light. We now know that light is not necessary for the growth and ripening of many species. This partial eversion of the pileus in many species unquestionably serves a useful purpose in providing for the wider distribution of the spores, for they are more easily caught by currents of air as they leave the hymenium.

The order in which elongation of the different parts takes place is thus different from the order of their initiation in the young primordium. As has been shown in these cultivated forms of *Agaricus campestris*, the organization of the primordia of pileus, stem, hymenium, and marginal veil is practically simultaneous by the appearance of the hymenial primordium as an internal annular area; while the organization of the parts gradually proceeds and is also simultaneous to a certain degree. But the period of elongation of the parts after they have become organized, while overlapping to a certain extent, follows in succession. The marginal veil completes its period of elongation first, then the stem, followed by the pileus, and finally the hymenium.

One striking feature of the hymenium of these cultivated forms is that, so far as I have examined (the varieties Columbia, Alaska,

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[27] See Nees von Esenbeck, Das System der Pilze und Schwämme 179–187. 1816.

Bohemia, and others), the basidia are two-spored. I have several times observed this fact in the cultivated mushroom. The illustration of the hymenium of *Agaricus campestris* which I have used on two former occasions[28] was made from a cultivated variety. GOEBEL'S *fig. 90*[29] shows only two spores on the basidium of *Agaricus campestris*, and this was probably also made from a cultivated variety. I have on the other hand several times observed that in case of the normal field or pasture form of *Agaricus campestris* there are four spores on a basidium. The nuclear phenomena in the formation of the spores have not yet been thoroughly worked out in the two-spored forms of *Agaricus campestris*, but studies of C. E. LEWIS carried on in my laboratory seem to show that the normal number of four nuclei are first formed in the basidium, and that two of them degenerate. This has been very clearly shown by him to be the case in a new species of Amanita, *A. bisporigera* Atkinson.[30] Nor has it been shown how the two-spored forms of *Agaricus campestris* arise from the normal four-spored feral plant, or whether normal two-spored forms exist as constant types in the field under natural conditions of environment. I have found a two-spored Agaricus resembling in some respects certain of the cultivated forms of *Agaricus campestris* growing spontaneously in the open. On one occasion it was found in June about young trees in a lawn which had been mulched with horse manure. On another occasion the same species was found on the hillside of a wooded ravine (Cascadilla gorge) on the campus of Cornell University.

If there are two-spored forms of *Agaricus campestris* existing under natural conditions of environment which are constant and which present also other characters even slightly different, it would indicate that *Agaricus campestris* either is or recently has been passing through a mutating period, and that these forms are elementary species. Were the two-spored basidia the only differentiating character, such a form might in the sense of DEVRIES[31] be regarded as

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[28] Studies and illustrations of mushrooms. I. Cornell Univ. Agr. Exp. Sta. Bull. 168. *fig. 189.* 1897; and Studies of Am. fungi, etc. (*l.*)

[29] Outlines of classification and special morphology, Eng. ed., 1887.

[30] LEWIS, C. E., The development of the spores in *Amanita bisporigera* Atkinson. BOT. GAZ. **41**:348–352. 1906.

[31] Species and varieties, their origin by mutation. 1905.

a variety, for it would seem that the four-spored quality or character is latent, since four nuclei are probably formed in the basidium in the normal manner but only two of them function. With regard to the cultivated forms of *Agaricus campestris* they probably represent also mutations either from *Agaricus campestris* or from some other species which has been confounded with it. Whether they are to be considered elementary species or varieties or retrograde varieties would depend upon their constancy or inconstancy, their stability or instability. They may be horticultural or domesticated varieties. Nevertheless it would seem that they have arisen by mutation. It is interesting to note in this connection that, whether species or varieties, if they have arisen by mutation their chances of becoming constant may be greater than in the case of plants which are well known to reproduce sexually. It is generally believed that the Agaricaceae are not reproduced by the cooperation of sexual organs. If this is true, and if there is no process similar to fertilization, mutations of these plants would escape one of the operations in nature against the constancy of new mutants in species capable of cross fertilization. Some students regard the fusion of the two primary nuclei in the basidium as an act of fertilization, but from what we know of the origin of these two nuclei the possibility of cross fertilization of individuals at this epoch of development is excluded, though it cannot at present be regarded as impossible at an earlier stage in their ontogeny. Of course the earlier ideas of fertilization in the Agaricaceae held in the time of BULLIARD,[32] who called the cystidia spermatic vessels and thought they squirted their juices on the seeds (spores) thus bringing about fertilization, or by CORDA[33] who regarded the cystidia as pollinaria and thought fertilization was brought about by the exudation of their fluid content to which the spores became attached and fertilized, are now unthinkable, as well as the notion of W. G. SMITH[34] as late as 1875, who believed that filaments growing out from the cystidia came in contact with the spores and fertilized

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[32] BULLIARD, Histoire des champignons de la France **1**:39–66. 1791.

[33] CORDA, Berich. Ises. **6**:40. 1834; also Icones **3**:44. 1839. See also H. HOFFMANN, Pollinarien und Spermatien bei Agaricus. Bot. Zeit. **14**:137–148, 153–163. *pl. 15*. 1856.

[34] SMITH, W. G., Reproduction in *Coprinus radiatus*. Grevillea **4**:53–65. *pls. 54–61*. 1875.

them, and that hybrids between species were very commonly found where cystidia and spores from adjacent species fell to the ground, commingled, and brought about cross fertilization. But the last word may not yet have been said with reference to the possibility of a fertilization prior to or during the early stages of the organization of the primordium of the carpophore, like that proposed by OERSTED (*l. c.*) for *Agaricus* (*Crepidotus*) *variabilis*, or in some closely related manner.

However, the propagation of forms by spawn which is not obtained from the spores, as is practiced by DUGGAR,[35] would seem to be equivalent to vegetative propagation or budding, and thus might be of advantage in maintaining constancy in varieties, since they would not be subject to cross fertilization, though it is still a question if fertilization and cross fertilization take place in the Agaricaceae. If it does not, or if some process equivalent to it, especially cross fertilization, does not take place, the Agaricaceae, and in fact the Hymeniales, would be especially free from the production of hybrids, and the constancy of species or varieties arising by mutation would be correspondingly favored. In a number of species there are indications that mutation is now going on, or that these species have recently passed through a period of mutation, and some of these apparent mutants appear to be quite constant. On the other hand, there are many species which show great fluctuating variability due to varying conditions of food supply, moisture, substratum, etc.

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DESCRIPTION OF PLATES VII–XII.

Photomicrographs with Zeiss microscope except *fig. 11;* plate holder 360^{mm} from object on slide; photomicrographs and photographs by the author.

PLATE VII.

FIG. 1. Young carpophore, var. Alaska, undifferentiated; oc. 2, obj. 16^{mm}.

FIG. 2. Same as *fig. 1*, but with oc. 4, obj. 16^{mm}.

FIG. 3. Young carpophore, var. Columbia, with primordium of hymenium in earliest stages of endogenous origin; oc. 2, obj. 16^{mm}.

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[35] DUGGAR, B. M., The principles of mushroom growing and mushroom spawn-making. U. S. Dept. of Agr., Bureau of Plant Industry, Bull. 85. pp. 9–60. *pls. 1–7.* 1905.

FIG. 4. Young carpophore, var. Alaska, with endogenous primordium of hymenium a little more advanced than in *fig. 3;* universal veil distinct as a loose definite layer of tissue surrounding the carpophore; oc. 2, obj. 16^{mm}.

FIG. 5. Young carpophore, var. Columbia, showing endogenous primordium of hymenium a little more advanced than in *fig. 4;* universal veil as a very thin layer; oc. 2; obj. 16^{mm}.

PLATE VIII.

FIG. 6. From young carpophore, var. Columbia; at stage when gill slit is just forming, showing sharp-pointed threads of primordium of hymenium projecting downward; also shows at the right the thin layer of universal veil; about same magnification as *fig. 7*, but not with Zeiss microscope.

FIG. 7. Same object as *fig. 6*, but showing only the gill slit and primordium of hymenium.

FIG. 8. Same as *figs. 6, 7*, but more highly magnified; oc. 6, obj. 3^{mm}.

PLATE IX.

FIG. 9. Young carpophore, var. Alaska, showing endogenous primordium of hymenium on one side, about the same stage as *fig. 4*, but higher magnification; oc. 4, obj. 16^{mm}.

FIG. 10. Young carpophore, var. Alaska, with endogenous primordium more advanced, showing definite and clear opening, the descending threads of the primordium of the lamellae, loose tissue of the inner veil, and primordium of stem cortex, outlined as an oblique area of younger threads rich in protoplasm, extending from opening obliquely downward and outward; oc. 6, obj. 3^{mm}.

FIG. 11. Portion of young carpophore, var. Columbia, showing gill slit; young lamellae in longitudinal section, inner veil of more open loose tissue; shows also how primordium of hymenium continues in its development as margin of pileus continues to grow; cortex of stem well-formed, showing as a more compact tissue over the surface to which the veil is attached; oc. 4, obj. 16^{mm}.

FIG. 12. Portion of young carpophore same age as *fig. 11* and from same plant, but cut somewhat obliquely so that a number of gills are shown in oblique section, otherwise as in *fig. 11*, but with less magnification; oc. 2, obj. 16^{mm}.

PLATE X.

FIG 13. Cluster of young carpophore, var. Columbia; numerous very young ones, several in the large button stage, showing the small white patches of the universal veil on the brown cuticle of the pileus.

FIG. 14. Another cluster of young carpophores, var. Columbia, showing numerous very small ones, and several of the small button stage, the universal veil separated into a few large white thin patches; rhizomorphs in the substratum.

PLATE XI.

FIG. 15. Longitudinal section of young carpophores magnified twice the real length, showing endogenous primordium of hymenium, gill slits, veil, and the primordium of cortex of stems.

FIG. 16. Real size; young carpophores, var. Columbia, showing rhizomorphs, the expanding young pileus and universal veil separated into patches; it is very distinct in the two plants where the universal veil is stretched between the two caps; at the right a few in longitudinal section.

FIG. 17. Young carpophore, var. Columbia, about half grown, real size, showing a few white patches of universal veil on the pileus, about midway of the short stem showing a ring which is the lower part of the double ring; in this case separated from the upper part and remaining on the stem as a distinct ring as in *Agaricus rodmani;* upper portion of the veil still attached from stem to margin of pileus which is as yet close against the stem.

PLATE XII.

FIG. 18. Cluster of mature carpophores of *Agaricus campestris,* cult. var., showing patches of universal veil on pileus.

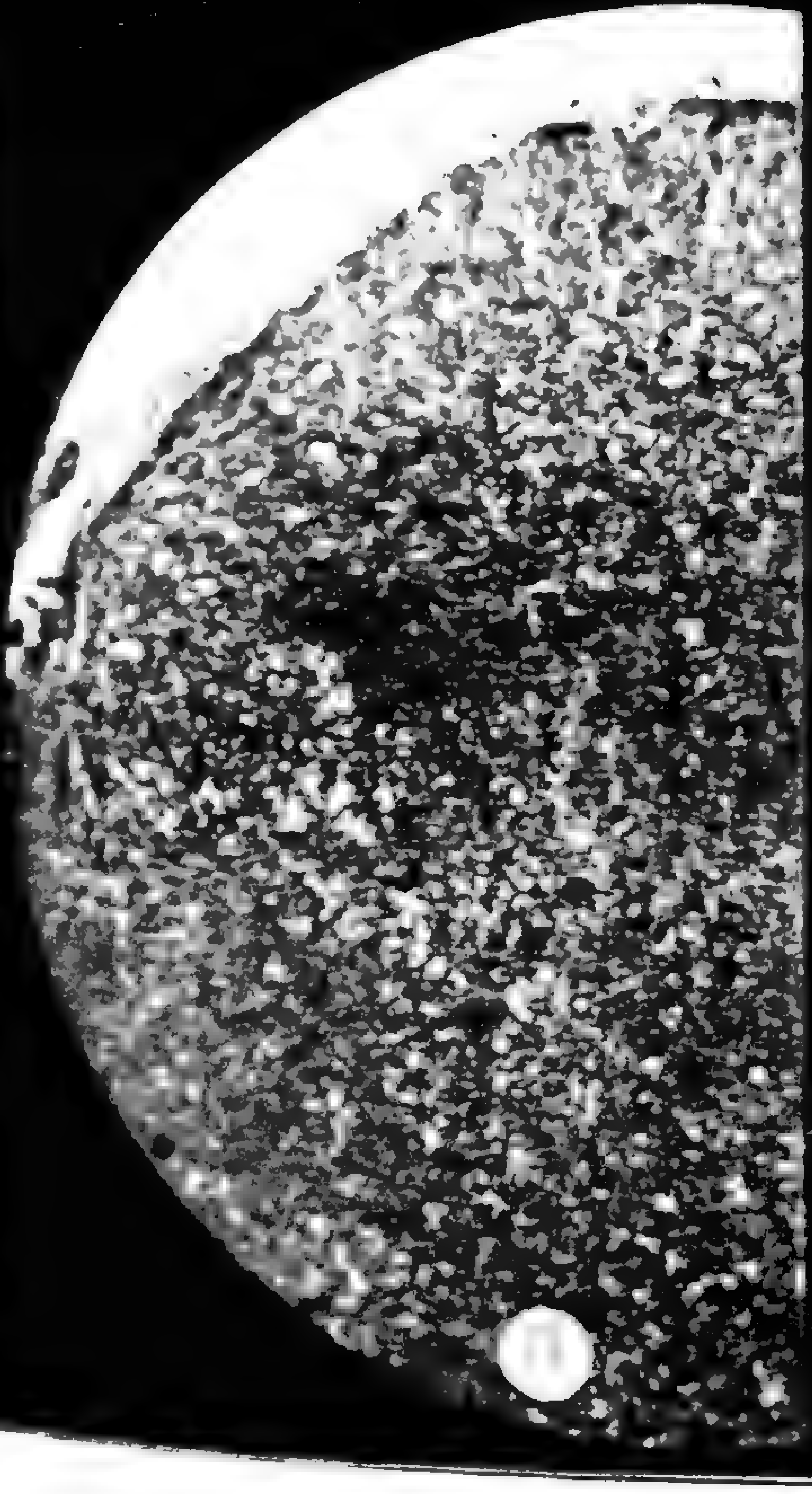
FIG. 19. Mature and nearly mature plants, var. Columbia, showing thick veil which forms a sterile margin on the edge of the pileus and a thick ring wrinkled or corrugated on the upper surface and the edge distinctly double.

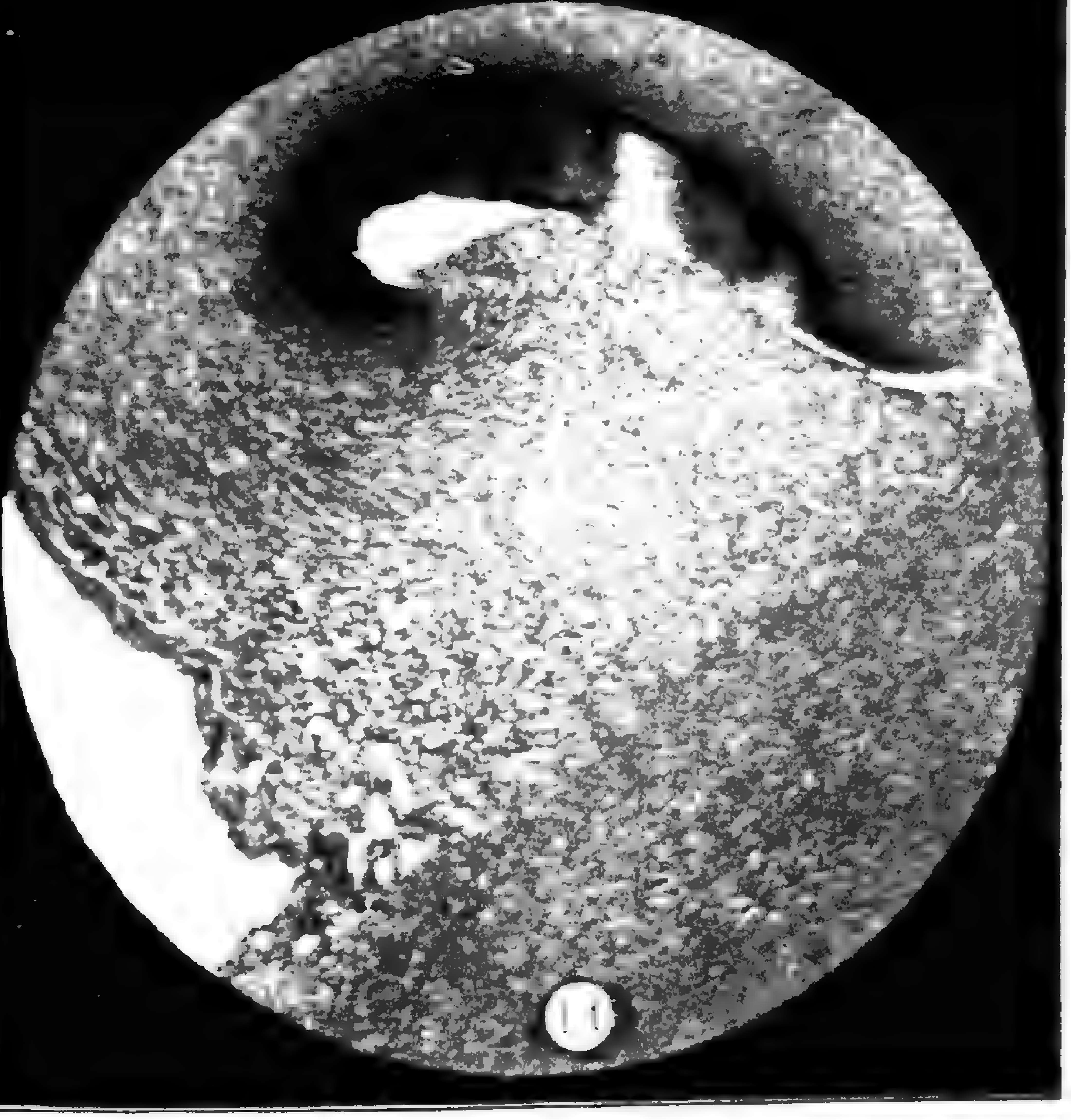
FIG. 20. Slightly younger stage, also lower part of double veil as broken away from the outer surface of margin of pileus; upper part of double veil still attached to margin of pileus.

The material was selected and fixed in chromo-acetic acid by myself, and I am under many obligations to Dr. CHARLES E. LEWIS, who then took the material, carried it into paraffin, sectioned, and stained it.

ATKINSON on AGARICUS

ATKINSON on AGARICUS





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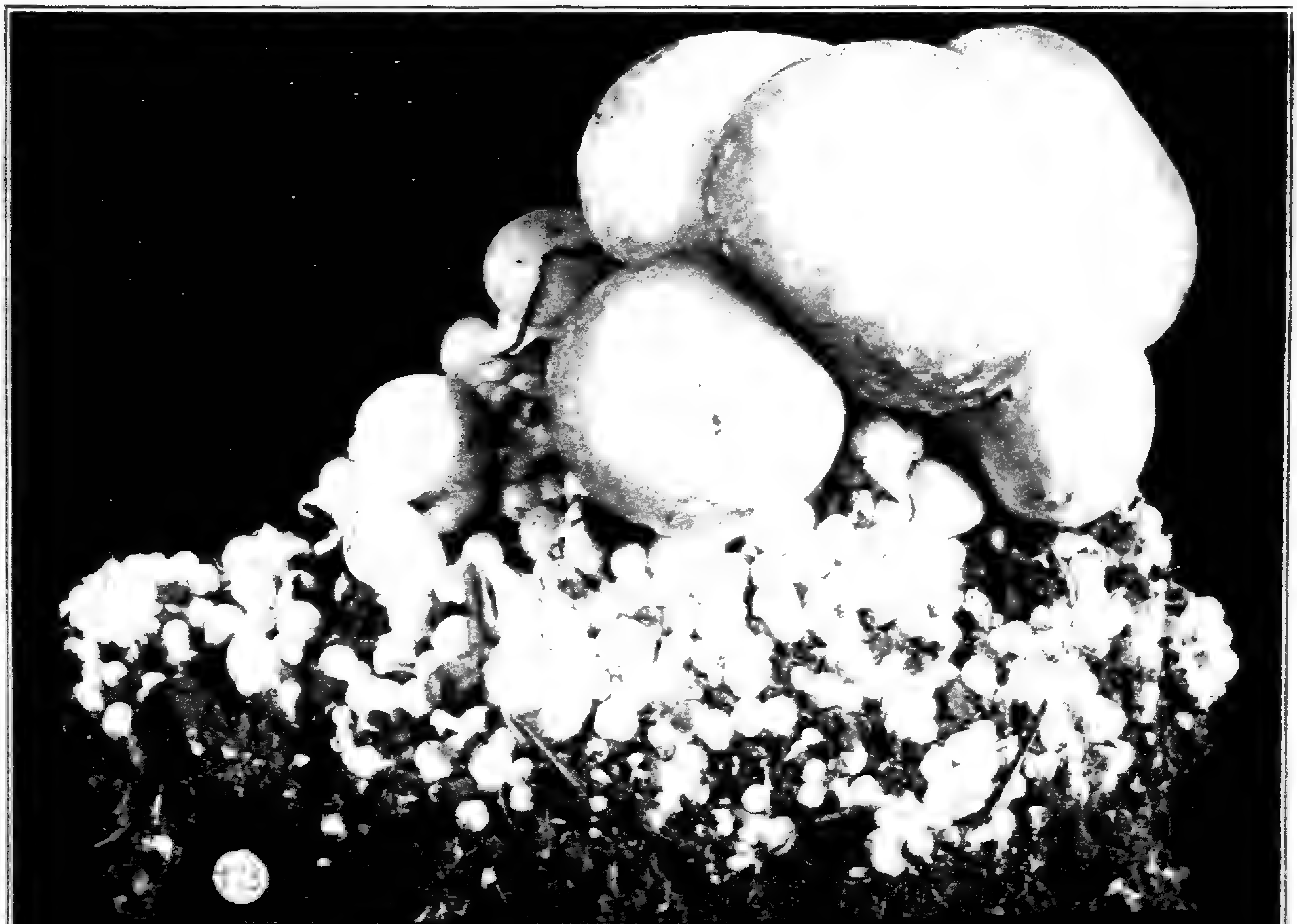

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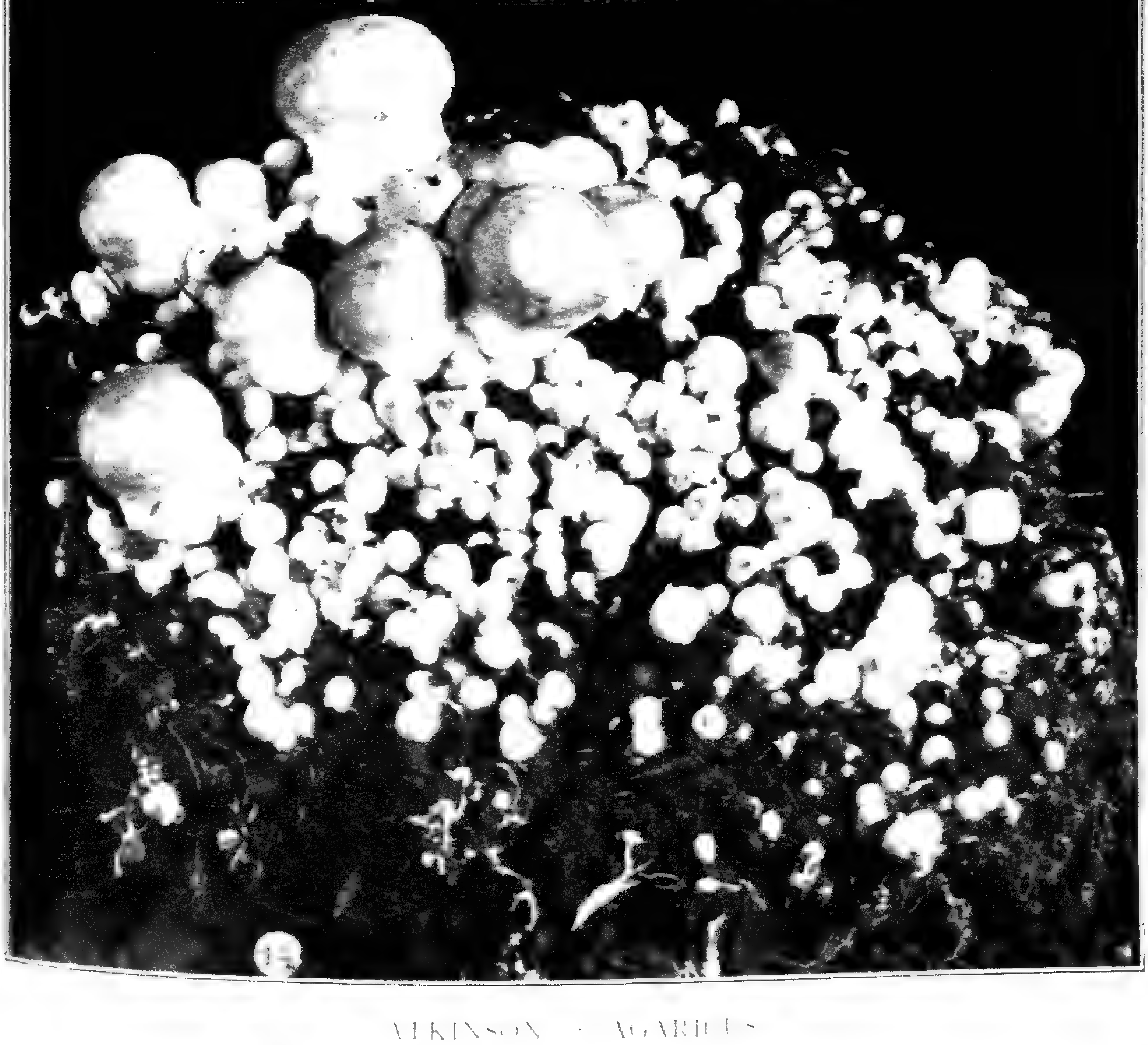

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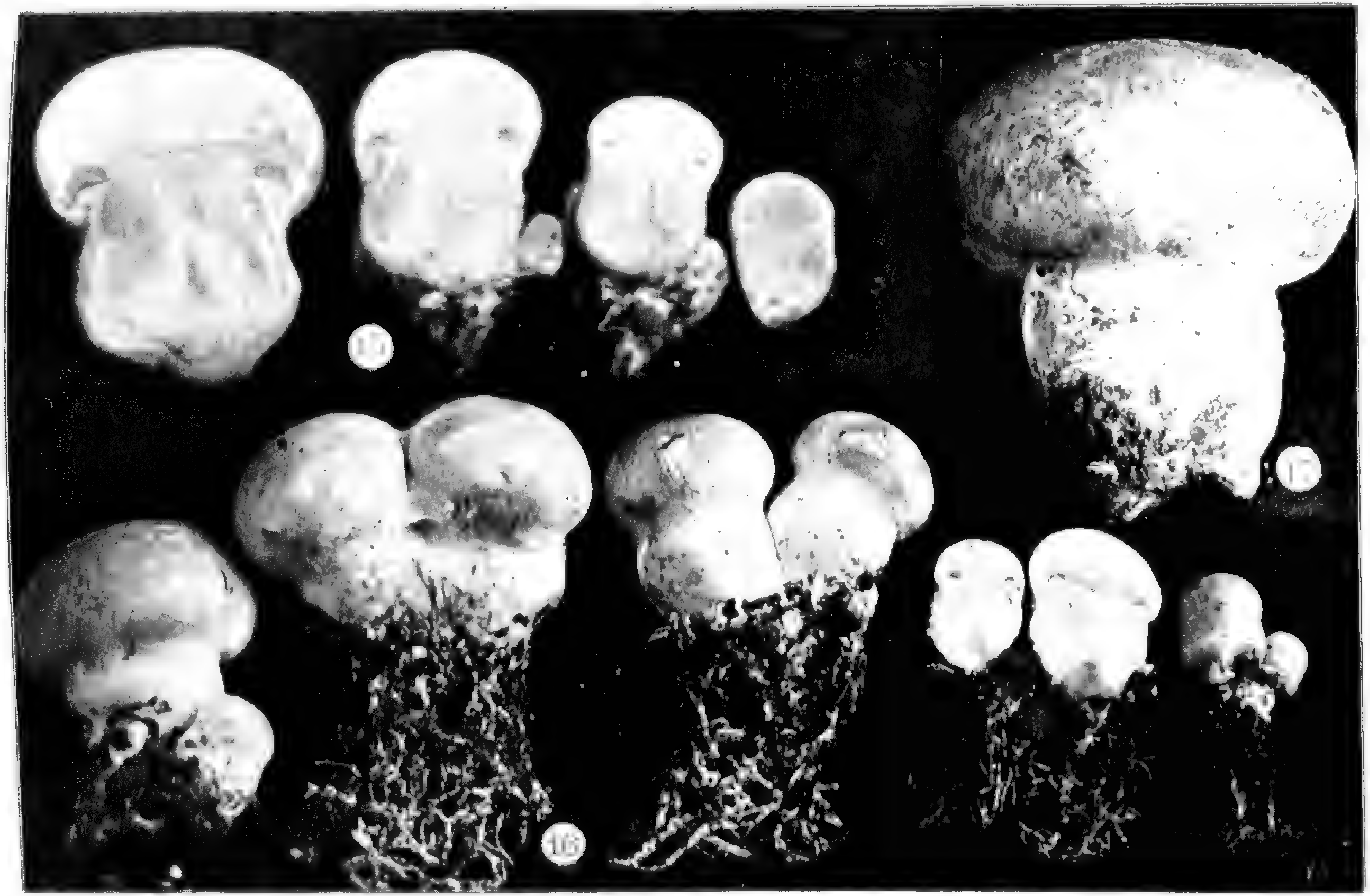

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RÔLE OF SEED COATS IN DELAYED GERMINATION.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXXXV.

WILLIAM CROCKER.

(WITH FOUR FIGURES)

I. Historical.

IT is well known that in many species of plants not all the seeds of a given crop germinate promptly after being subjected to so-called germination conditions; instead they germinate at irregular intervals through a period of weeks, months, or even years. It happens in many species that none of the seeds of a crop will germinate until they have been subjected to germinative conditions for a year or more, and that in these cases of marked delay germination is distributed through a further period of greater or less length.

Delayed germination is well illustrated in the results of the researches of NOBBE and HÄNLEIN (**8**, *a*, *b*). Table I shows their observations on thirty-one species of common weeds. They began with 400 seeds of each species and continued their experiments 1,173 days.

KIENITZ (**4**) found marked distribution in the germination of crops of the beech, white fir, ash, hornbean, and pine; and WINKLER (**15**) in sowings of *Euphorbia cyparissias*, *E. exigua*, Cuscuta, etc. WIESNER (**14**) found that the seeds of *Viscum album* germinate only sparingly in the fall after ripening, but readily the following spring. KUNTZE (**6**) in reviewing the literature on germination mentions a large number of cases of delayed germination. The hawthorn, he states, will grow only after being in the ground one to three years.

One of the most interesting cases of delayed germination is that of the cocklebur (Xanthium) reported by ARTHUR (**1**). He found that the two seeds in the bur are not the exact counterparts of each other, but can be distinguished readily by their form and position in the bur. One seed, which he terms the upper because it is borne nearer the apical end of the bur, is convex on the outer face and con-

TABLE I.

AFTER NOBBE AND HÄNLEIN; 400 SEEDS OF EACH SPECIES.

Name. No. of seeds germinated on day	4	5	6	7	8	9	10	16	36	72	145	351	519	714	874	1082	1173	Total	Per ct.
1 Aquilegia vulgaris	..	..	..	...	...	...	..	3	..	..	..	..	...	...	...	...	...	3	0.75
2 Campanula rotundifolia	..	..	..	11	8	1	1	1	1	..	..	..	11	13	10	1	...	58	14.50
3 Campanula persicifolia	..	..	..	...	3	8	14	112	56	1	..	11	9	2	8	2	6	232	58.00
4 Campanula Trachelium	..	..	..	...	...	...	..	...	..	..	..	..	1	...	...	...	...	1	0.25
5 Chaerophyllum temulum	..	..	..	...	...	...	..	...	..	..	..	..	...	...	...	...	3	3	0.75
6 Chenopodium album	..	..	2	...	...	2	3	2	..	1	19	53	27	...	2	3	3	117	29.25
7 Capsella Bursa-pastoris	..	3	..	3	...	...	..	...	..	..	4	4	20	...	24	10	7	75	18.75
8 Chelidonium majus	..	..	..	...	...	...	..	...	59	8	2	..	...	3	90	1	32	195	48.75
9 Digitalis purpurea	..	..	..	9	45	102	47	159	24	1	..	..	...	...	rest	eca	yed	387	96.75
10 Hypericum hirsutum	..	..	..	2	1	4	13	132	58	..	..	2	...	...	...	...	...	212	53.00
11 Hypericum montanum	..	..	..	3	19	61	31	171	46	..	..	..	...	1	...	...	...	332	83.00
12 Hypericum perforatum	..	..	..	1	...	...	2	20	28	2	..	..	...	1	3	1	...	58	14.50
13 Jasione montana	..	..	17	98	141	81	30	28	2	..	..	..	...	...	rest	deca	yed	397	99.25
14 Lithospermum arvense	2	12	32	36	52	18	8	52	42	28	22	12	22	6	rest	deca	yed	344	86.00
15 Lysimachia vulgaris	..	..	..	...	...	...	..	...	..	..	..	..	...	1	...	...	...	1	0.25
16 Myosurus minimus	..	..	16	160	103	19	2	5	..	1	..	11	11	4	13	...	2	347	86.75
17 Oxalis corniculata	..	..	..	...	...	...	..	3	5	1	..	1	...	...	2	...	...	12	3.00
18 Papaver Argemone	..	..	5	65	116	16	8	34	30	15	4	26	17	...	...	...	...	336	84.00
19 Papaver dubium	..	..	2	216	169	...	..	1	..	..	..	..	...	...	...	...	...	388	97.00
20 Phyteuma spicatum	..	..	..	...	...	...	..	...	..	..	..	..	...	...	...	...	...	0	0.00
21 Plantago major	..	..	..	...	...	...	..	...	..	..	..	..	...	...	...	...	1	1	0.25
22 Plantago media	..	5	8	4	4	2	1	...	..	..	..	1	...	9	1	6	2	43	10.75
23 Polygonum persicaria	..	3	33	15	2	...	..	2	..	..	..	..	...	...	...	...	...	55	13.75
24 Primula elatior	..	..	..	...	...	...	..	...	..	..	..	..	...	...	...	...	...	0	0.00
25 Potentilla argentea	..	..	3	15	57	67	58	74	7	..	..	2	3	3	3	2	7	301	75.25
26 Scrophularia nodosa	..	..	1	5	27	96	42	47	6	..	..	..	...	...	7	...	...	231	57.75
27 Thlaspi alpestre	..	..	..	...	...	...	..	...	..	..	..	..	all	deca	yed	...	...	0	0.00
28 Thlaspi arvense	..	..	..	...	1	...	..	2	..	..	..	2	10	11	11	15	35	87	21.75
29 Verbascum nigrum	..	..	..	...	...	...	..	...	..	..	..	..	...	...	...	...	...	0	0.00
30 Veronica Beccabunga	..	..	..	...	...	...	..	1	1	1	6	25	42	103	...	4	...	183	45.75
31 Veronica officinalis	..	..	..	...	...	8	56	332	..	..	..	..	...	...	rest	deca	yed	396	99.00

cave on the inner. The lower seed, lying nearer the base of the bur, is concave on the outer face and convex on the inner. ARTHUR found that plantings of burs of the cocklebur (mainly *Xanthium canadense*) in a garden bed resulted in the germination of all the lower seeds in the first year after ripening, and of only a very small per cent. of the upper seeds. The second year a great majority of the upper seeds grew. A few of the upper ones, however, grew in the third and fourth years.

MASTERMAN (**7**) claims that both seeds grow the first year after they are planted. His methods, however, were not at all adapted for detecting whether the two seeds of the bur have markedly different germinative characters. Both ARTHUR'S work and the experimental results of this paper show that such differences in the germinative characters undoubtedly exist.

FIG. 1.—Cocklebur cut away to show upper and lower (dimorphic) seeds.

Delayed germination was found by NOBBE and HÄNLEIN to be due in many cases to the impermeability of the seed coat to water. As to the seeds listed in Table I, however, they say that in every case the seeds absorbed the water readily and yet lay in the germinator in a saturated condition for long periods, either not germinating at all or scattering their germination over a long period. They maintain that in cases where water is admitted the growth after long exposure to germinative conditions must be due to some change going on within the embryo during the period of rest. WINKLER (**15**), WIESNER (**14**), KIENITZ (**4**), and PFEFFER (**9**) expressed similar views.

ARTHUR found that both seeds of the cocklebur take up water readily while in the bur. The bur, therefore, does not account for the delay. He also believes that the extremely delicate seed coats are in no way different in the two seeds and that the structure of the seeds, therefore, offers no explanation of their germinative difference.

He suggests that enzymes are produced readily in the lower seeds and that, therefore, they have foods at hand to begin their growth immediately; whereas the upper seeds are able to develop digestive ferments only after a long period of rest, and hence their germination is delayed one or more years. This theory has its experimental basis in the fact that if both sorts of seeds are exposed to germinative conditions for some time the lower ones show much reducing sugar, while the upper ones have only a trace. My interest in this problem was aroused by ARTHUR'S paper on the cocklebur, and the work was begun for the purpose of testing this enzyme theory and determining definitely the cause of the delayed germination of the upper seed.

II. Materials and methods.

Most of the germinative tests reported in this paper were made between moist filter papers, but in all these cases corresponding tests with very similar results were made in fine quartz sand and in garden soil. For *Avena fatua*, Iris, and cocklebur seeds in the bur, all tests were made in sand and garden soil on account of the great liability of these structures to be attacked by fungi.

Five species of cocklebur were used: *Xanthium canadense* Mill., *X. echinatum* Murr., *X. glabratum* (DC.) Britton, *X. glanduliferum* Greene, and *X. speciosum* Kearney. In each species similar conditions gave similar results whether the seeds were in the bur or removed from it; but for convenience in handling and accuracy of the records the seeds were generally removed from the bur. For testing increased oxygen pressures the soaked seeds were allowed to rest on the walls of flasks containing oxygen or (in the checks) air. Germinative tests at high temperatures were made in ordinary paraffin ovens regulated to the desired temperature. The effect of temperature on the rate of diffusion of oxygen through the seed coats of the cocklebur was determined in a large water bath (such as is used in chemical laboratories for determining solubility, etc.) regulated to 0.01°.

The seeds used were collected when thoroughly ripe from various parts of the United States and Europe,[1] stored in a dry room, and used in experimentation within six months after collected. Since a year of dry storage and the region from which the seeds were

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[1] I am indebted to M. P. DIEUDONNÉ for collections from Belgium.

gathered gave no marked germinative variations in the species used, the time of storage and the region in which they were collected need no further consideration. A seed was considered germinated when root hairs appeared, except in Xanthium and Iris, where late development of root hairs made this test worthless and the lengthening of the radicle 5^{mm} was considered the criterion of germination.

III. Experiments.

1. COCKLEBUR.

Effect of enzymes.—When work was begun on the seeds of the cocklebur, ARTHUR'S enzyme theory was adopted as a working hypothesis, on the supposition that it would involve a study of the difference in the development and action of the enzymes in the two seeds. As WAUGH (**13**), STONE (**10**), and THOMPSON (**11**) were able to increase markedly the germination of old seeds by soaking them in solutions of various enzymes, it was thought that perhaps the upper seeds of the cocklebur could be made to germinate without delay by merely soaking them in solutions of pepsin, or plant trypsin, or in filtered extracts from the germinated lower seeds. Experiments in this line gave only negative results, but led to the discovery that high temperatures cause the immediate germination of some of the upper seeds. The enzyme theory was abandoned after failures to detect any differences in the digestive activities of extracts of the upper and lower seeds. At this point the results showed that the difference in the germinative characters of the two seeds had other causes; hence a new line of experiments was begun.

Effect of high temperatures.—High temperatures bring about the immediate germination of the upper seeds of *X. echinatum.* Table II shows the results of temperature experiments with this species. Results were similar whether soil or filter paper was used for germinators and whether the seeds were in the burs or removed from them.

As Table II shows, the lower seeds of *X. echinatum* germinate readily at 22–24°, but even more readily at 32–34°. The upper seeds do not germinate at all at 22–24°, but respond readily at 32–34°. The lowest temperature at which any considerable per cent. of the upper seeds grow is at 33°, and the similar point for the lower seeds

TABLE II (*X. echinatum*).

TEMP. °C.	SEEDS	PER CENT. GERMINATED AFTER			
		1 day	2 days	5 days	8 days
22–24	upper	0	0	0	0
	lower	3	31	87	99
32–34	upper	8	55	99	99
	lower	23	100	100	100

is 23°. In *X. canadense*, *X. glabratum*, and *X. speciosum* the upper seeds germinate only sparingly at a constant temperature of 35°, but to a considerably larger per cent. at a temperature fluctuating between 25 and 40°. The lower seeds of *X. canadense* germinate readily at 18–21°, while the lower seeds of *X. glabratum* have a minimum germinative temperature of about 23°. The highest minimum germinative temperature yet reported, 15.6–18.5°, is recorded by DETMER (**2**) for the cucumber and watermelon.

From the above data it may be seen that in the cocklebur there are remarkably high minimum germinative temperatures. *X. echinatum*, the least remarkable of the four species studied in this respect, has this critical temperature 15° higher in the upper seed and 5° higher in the lower one than that of the watermelon and cucumber.

Effect of wounding.—In removing seeds from the burs the knife often clipped off a small portion of the distal ends of the cotyledons. It was observed that the upper seeds so wounded begin a marked growth in the wounded region even at the temperature of 20–22°. The growth gradually moves down the cotyledons until it reaches the radicle. This reverses the normal method of germination. Normally the radicle first pushes out, sets itself in the ground, and lifts the cotyledons above the soil, after which they begin their growth. When the upper seeds are wounded at the radicle end, either by a slight cut or a pin prick, germination takes place in the normal way. This observation suggested complete removal of the seed coat.

Effect of removing the seed coat.—After the seeds have been soaked six hours the extremely delicate seed coats can be removed, without the least injury to the embryo, by merely pinching the seed between thumb and finger. The coat-free upper and lower seeds of any one of the four species studied germinate with almost equal readiness at any point within their temperature limits, and the two seeds have almost identical temperature limits. Table III shows the relative speed of germination of the upper and lower seeds of *X. canadense* at 18–22°. The minimum germinative temperature for the upper and lower seeds of this species with the seed coats removed is about 18°. The same point for other species mentioned is 2–3° higher. Each seed of Xanthium has then two minimum germinative temperatures: one with the seed coat intact, and a lower one with the seed coat removed. In the upper seeds these two temperatures differ by fifteen or more degrees and in the lower ones by two or more degrees. Table IV gives the approximate germinative minimum temperatures for each of the four species with seed coats intact and seed coats removed.

TABLE III.

X. canadense; COATS REMOVED; TEMP. 18–22°.

SEEDS	PER CENT. GERMINATED AFTER			
	3 days	4 days	6 days	9 days
Upper........	47	75	84	100
Lower........	51	77	89	100

TABLE IV.

MINIMUM GERMINATIVE TEMPERATURES.

Species	Seeds	Minimum temp. °C. coats intact	Minimum temp. °C. coats removed
X. canadense............	upper	fluctuating 25–41	18
	lower	21	18
X. echinatum...........	upper	32–33	19–20
	lower	23	19–20
X. glabratum............	upper	fluctuating 25–41	20
	lower	23	20
X. speciosum...........	upper	fluctuating 25–41	20
	lower	22	20

It is evident from the results so far given that ARTHUR'S statement that the difference between the two seeds does not lie external to the embryo, but in the embryos themselves, is entirely wrong. He overlooked the real point of difference, the seed coats, because of their extreme delicacy and because of the ease with which they admit water.

Effect of increased oxygen pressures.—Since the delay is secured by the seed coat, it must exclude either water or oxygen. As ARTHUR states, both seeds seem to take up water with equal readiness. I found that in eighteen hours of soaking, the upper seeds of *X. canadense* imbibed 51 per cent. of their dry weight, while the lower ones imbibed 62 per cent. In the same time the upper seeds of *X. echinatum* imbibed 48 per cent. and the lower ones 47 per cent. The difference then in water imbibition will not serve to explain the difference in the germinative characters of the two seeds.

It was found best in testing increased oxygen pressures to soak the seeds 12–18 hours and then allow them to stick to the walls of a flask or bottle containing the oxygen or (in the check) air. After being thus treated and kept at 21–23° for six days, the upper seeds of *X. canadense* gave 100 per cent. of germination in pure oxygen and 0 per cent. in air. The growth in the seeds germinated in oxygen at these relatively low temperatures does not take place in the normal way. It begins in the distal region of the cotyledons and works down toward the radicle, as was described for seeds wounded at the distal end of the cotyledons. This peculiarity seems to be related to the structural character of the seed coat.

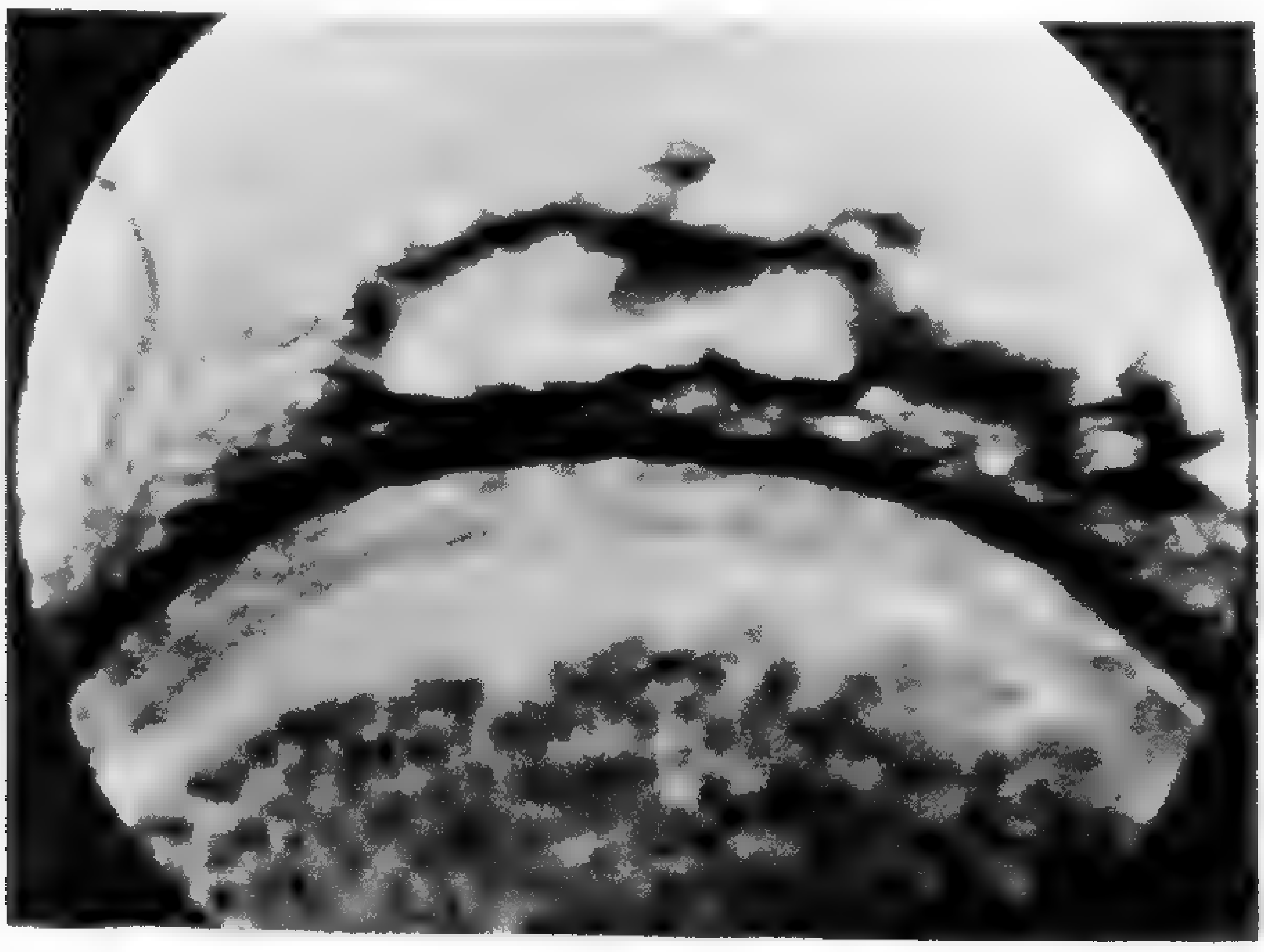

FIG. 2.—Cross section of the seed coat of Xanthium, showing the three layers.

The seed coat consists of three distinct layers (*fig. 2*). The outer layer consists of shell-like cell walls which are more and more collapsed as the inner portion of the layer is approached. This layer is traversed by several groups of tracheae which are parallel with the long axis of the seed. The middle layer is very dense, apparently consisting of collapsed cell walls and staining very deeply with safranin. The inner layer consists of 1–5 layers of cells containing protoplasm and nuclei. Each layer is thickest at the radicle end and gradually becomes thinner toward the distal end of the cotyledons.

The measurements of the three layers are approximately as follows: the outer layer, at the radicle end 100 μ, at the distal end 20 μ; the middle layer, at the radicle end 15 μ, at the distal end 8 μ; the inner layer, at the radicle end 30 μ, at the distal end 4 μ. The middle layer is somewhat thicker in the upper than in the lower seed. In both seeds it is less dense at the distal end. It seems probable that the denser middle layer is only partly permeable to oxygen, less so in the upper than in the lower seed, and less so at the distal than at the radicle end. This accounts for the increased oxygen pressure initiating the growth at the distal end.

Gaseous exchanges in respiration.—The two sets of experiments on the gaseous exchanges of the seeds in respiration throw some light on the effect of the seed coats. The first set, reported in Table V, shows the ratio of the oxygen taken up with the seed coats removed to that taken up with the seed coats intact. Only the ratios can be compared here, for different weights of seeds were used in the four different determinations. These measurements were made with eudiometers.

TABLE V.

ABSORPTION OF OXYGEN; SEED COATS INTACT AND REMOVED; TEMP. 23°.

SEEDS USED	COATS	CC. OF OXYGEN TAKEN UP AFTER		RATIO OF I TO II	
		6 hrs.	22 hrs.	6 hrs.	22 hrs.
Lower seeds, X. canadense.............	removed I	2.5	12.6		
	intact II	1.6	6.9	1.6	1.8
Lower seeds, X. echinatum.............	removed I	12.2			
	intact II	7.1		1.7	
Upper seeds, X. glanduliferum..........	removed I	4.4	11.0		
	intact II	2.1	3.6	2.1	2.4
Upper seeds, X. echinatum.............	removed I	9.4	13.4		
	intact II	4.5	6.7	2.1	2.0

As Table V indicates, the lower seeds at 23° take up 1.6 to 1.7 times as much oxygen with the seed coats removed as with the seed coats intact; while the upper seeds take up 2 to 2.4 times as much oxygen with the seed coats removed as with them intact. The ratios are probably much smaller than would obtain in the soil or between wet filter papers, for the coats of the seeds lying on the walls of the eudiometer, though in a theoretically saturated atmosphere, became relatively dry. As is found by actual measurement, oxygen diffuses through the relatively dry seed coats much more rapidly than through those saturated with water. This is indicated again by the fact that the soaked upper seeds of *X. echinatum* germinate readily at 25–27° when resting on the walls of corked bottles containing air, while in soil or between saturated filter papers a temperature of 33° is necessary for any considerable germination. The upper seeds of every species with seed coats intact can be most easily germinated by allowing the seeds to lie on the walls of corked bottles of such size that a good oxygen supply is given. In this condition the relatively dry coats allow the passage of considerably more oxygen, hence germination comes about at lower temperatures.

The second set of experiments on gaseous exchange is for the purpose of determining why high temperatures bring about the germination of the upper seeds with the seed coats intact. It immediately suggests itself that this may be due to one or both of two things: the amount of oxygen diffusing through the seed coat may rise with the rising temperature, or the amount of carbon dioxide evolved may become greater in proportion to the amount of oxygen consumed as the temperature rises.

It is seen in the 6-hour 50-minute column, as well as in the 12-hour column of Table VI, that the seeds with the coats intact at 19°, whether upper or lower, take up less than half as much oxygen as is taken up by the seeds at 33°. This indicates that the diffusion of oxgyen through the seed coats is much slower at 19° than at 33°. This conclusion, however, needs more direct evidence. Especially is this apparent when it is remembered that 19° is slightly below the minimum germinative temperature, even with the coats removed, and that the amount of oxygen consumed, therefore, may not represent the full amount that can diffuse through the coats at 19°, provided the consumption on the inside is complete.

The apparatus in *fig. 3* was used for determining accurately the effect of high temperatures on the rate of diffusion of oxygen through the seed coats. *S* is a storage bottle for potassium pyrogallate; *j*, a flask from which the oxygen is to be absorbed by potassium pyrogallate; *t*, a seed coat fastened on the end of a glass tube; *w*, a vial of water from which a thread reaches the seed coat to keep it wet; *c*, a capillary tube sealed at the upper end with wax; *c'*, a small graduated tube by which the rate of diffusion of oxygen is to be ascertained; and *a*, an air chamber. After *s* is furnished with 300^{cc} potassium pyrogallate the whole apparatus, excepting pinchcock 1 and the portions of tubes *c* and *c'*, is immersed in a water bath regulated to the desired temperature within .01°. After the apparatus has had sufficient time to attain the temperature of the bath, pinchcocks 1 and 2 are loosened; the plugged end of *c* filed off; and the pryogallate forced into *f*. Now *c* is resealed and the pinchcocks reclamped; a drop of water is allowed to enter the graduated tube *c'*; and the rate of diffusion of the oxygen is read by the rate of the movement of the drop in tube *c'*. The same seed coat can be used repeatedly at temperatures to be compared. Numerous measurements made in this way showed the rate of diffusion 1.4 to 1.6 as fast at 33° as at 19°.[2]

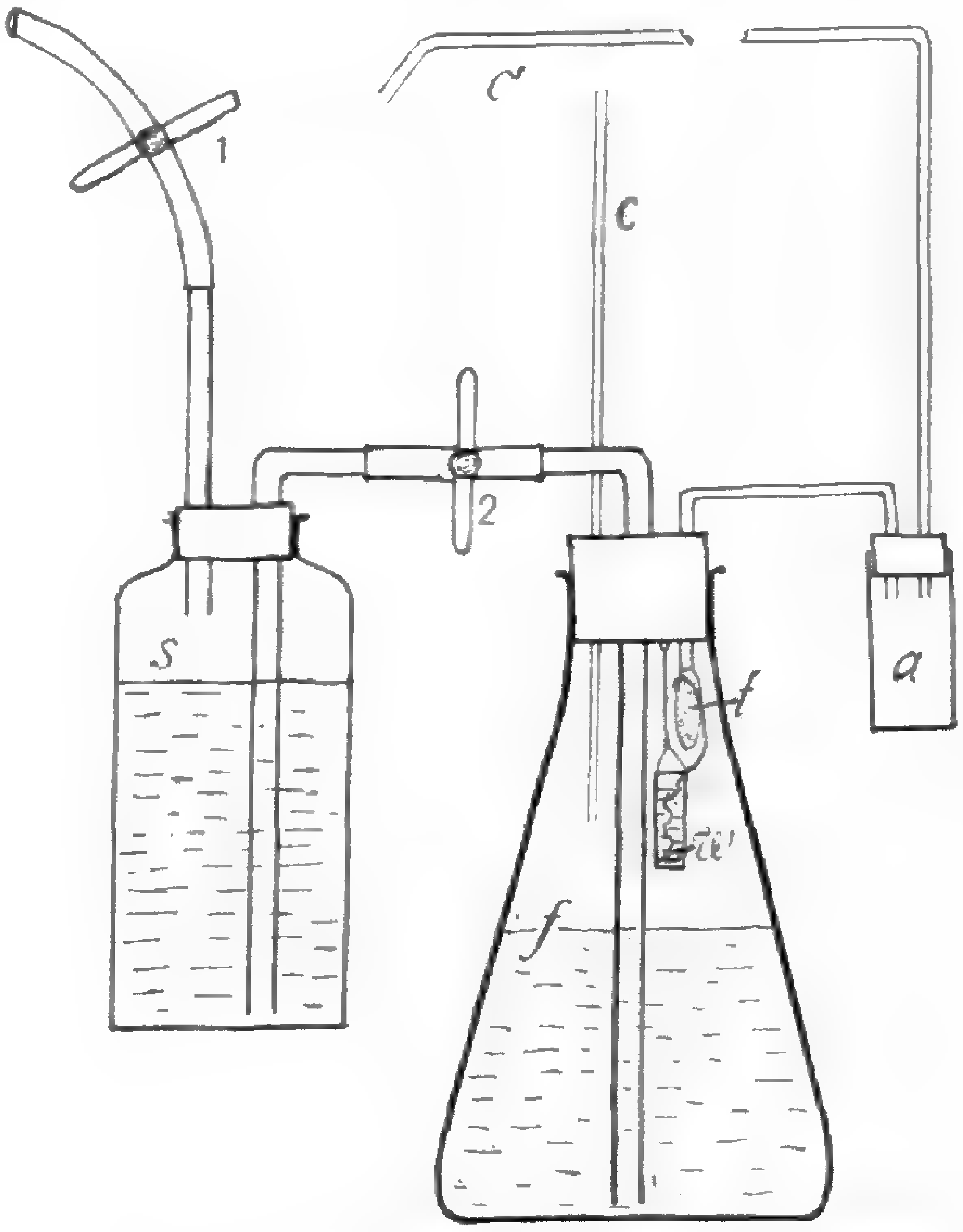

FIG. 3.—Apparatus for testing permeability of seed coats of cocklebur to oxygen. For description see text.

The amount of CO_2 evolved is considered the best measure for the amount of respiration occurring. It is evident from the measurements recorded above, that if the ratio $CO_2:O_2$ remains constant with the rise in the available oxygen due to the rise in temperature, the amount of carbon dioxide evolved will increase from 1 to 1.4–1.6 as the temperature rises from 19° to 33° with the seed coats intact. If it happens, however, that the ratio $CO_2:O_2$ rises in value along with the rise in the rate of the diffusion of oxygen, then the increase in respiration with this rise in temperature will be still more marked.

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[2] When the coat was allowed to dry somewhat the rate of diffusion was also greatly increased.

This involves the necessity of making a study of the respiratory ratios at 19° and at 33°, both with the coats intact and removed.

Table VI shows the effect of high temperatures on the respiratory ratios when the seed coats are intact. In this experiment equal weights (2.68^{gm}) of seeds of *X. echinatum* were used in each case. The results are therefore comparable in every way. It is seen that at 33°, up to the 6-hour 50-minute reading the respiratory ratio for both upper and lower seeds is 1. After this reading the ratio falls rapidly, reaching at the 12-hour reading 0.82 in the case of the lower seeds and 0.87 in the case of the upper ones. It was observed that soon after the 6-hour 50-minute reading the radicles began breaking through the seed coats. In a large number of experiments at 33° the respiratory ratio always fell rapidly after the radicles broke the seed coat. At 19°, with the seed coats intact, the respiratory ratio is 0.6 in the lower seeds and 0.64 in the upper ones. Many measurements at 33° with seed coats removed showed a respiratory ratio of 0.7–0.8 in both the upper and lower seeds, while numerous measurements at 19° with seed coats removed always gave a respiratory ratio of about 0.6.

The facts may be summarily stated thus: the respiratory ratio with the seed coats removed is about 0.6 at 19° and 0.7–0.8 at 33°; with the seed coats intact it is 0.6 at 19° and 1.0 at 33°. From these results two conclusions are plain: the respiratory ratio rises considerably (from 0.6 to 0.8) with a rise in temperature from 19° to 33° under the free oxygen supply secured by the removal of the seed coats; but it rises much more (from 0.6 to 1.0) with the same

TABLE VI.

X. echinatum—SEED COATS INTACT; 119 UPPER SEEDS; 88 LOWER; 2.68 GM.

SEEDS	TEMP. °C.	CC. INTERCHANGE OF GASES AFTER											
		4 hrs. 50 min.			6 hrs. 50 min.			10 hrs.			12 hrs.		
		O_2	CO_2	$\frac{CO_2}{O_2}$	O_2	CO_2	$\frac{CO_2}{O_2}$	O_2	CO_2	$\frac{CO_2}{O_2}$	O_2	CO_2	$\frac{CO_2}{O_2}$
Lower	33	3.3	3.3	1.	4.9	4.9	1.	7.9	6.5	.83	9.9	8.3	.82
Upper	33	2.8	2.8	1.	4.1	4.1	1.	6.	5.3	.88	7.1	5.9	8.7
Lower	19				1.8	1.1	.61				4.0	2.4	.60
Upper	19				1.5	.94	.63				3.3	2.1	.64

rise in temperature when the oxygen supply is diminished by the presence of the seed coats.

This rise in the respiratory ratios with the rise in temperature is measured for the entire seed (more than 95 per cent. of which is storage material) and not for the actively growing radicle. It is probable that for the radicle the respiratory ratio rises far above 1. This becomes more evident when it is remembered that at 33° the radicle grows first, as is normal; but that at 22°, in increased oxygen pressures, though it be five atmospheres, the growth of the cotyledons first takes place. Here, too, it should be recalled that the seed coat is much thicker and more dense over the radicle than over the cotyledons.

From the data of this section two effects of a rise in temperature are evident. It increases the rate of diffusion of oxygen through the seed coats; and it increases the respiratory ratio somewhat with the seed coats removed and markedly with the seed coats intact. If CO_2 be taken as the criterion, it is possible from the data above to calculate quantitatively the increase in respiration with a rise in temperature from 19° to 33°, when the seed coats are intact. The increase in the rate of diffusion of oxygen (if there were no increase in the ratio $CO_2:O_2$) equals an increase in respiration from 1 to 1.5 (the average of 1.4–1.6). But the increase in the respiratory ratio is from 0.6 at 19° to 1.0 at 33°. This then increases the respiration from 6 units to 10 units. When the two facts that indicate an increase in respiration are considered together, it is evident that a rise in temperature from 19° to 33° with the coats intact causes a rise in the amount of respiration from 0.6 to 1.5, or from 1 unit to 2.5 units.

It is evident from Table V that the seed coats of the lower seeds, as well as those of the upper, greatly restrict the amount of oxgyen used by the seeds, and that this restriction, though considerable, is not markedly greater in the upper seeds than in the lower ones. In *X. echinatum* this rather slight difference in the rate of diffusion of oxygen through the seed coats of the upper and lower seeds is yet sufficient to give the upper seeds a minimum germinative temperature of 32° with seed coats intact, and the lowers 22°; while both seeds with the seed coats removed have a minimum germinative temperature of 19°. Since the difference of the two seed coats in the matter of oxygen diffusion is rather slight, it is not remarkable that the structural difference is not radical. This slight difference, however, is sufficient to raise the minimum germinative temperature and secure the delay of the upper seed.

Growth of upper seeds.—It is now obvious how the *delay* of the upper seeds is secured. But why do they grow at all in nature? This comes about by a partial disintegration of the seed coats, which is clearly shown by a change in appearance from shiny brown to a dull black or in some cases to colorless, and results in the admission of more oxygen. The length of the delay depends upon the ability of the seed coat protected by the surrounding bur to resist the factors of disintegration in the soil. The portion of the bur covering the lower seed decays within a few months after burial, while the portion covering the upper seed is always far more persistent. A variation in the persistence of the portion of the bur covering the upper seed, as well as the variation in the ability of the seed coat to resist the factors of disintegration independent of the bur, gives considerable variation in the length of delay of the upper seed. These facts show why only a few of the upper seeds grow the first year after ripening, the vast majority the second year, and a few not until the third and fourth year.

Table VII shows the effect of a period in the ground upon the seed coats and upon the vitality of the embryos of the upper seeds of *X. canadense.* Burs produced in 1904 were gathered in November of that year and stored in the laboratory until March 1905. At this time half these burs were buried and the other half kept in the laboratory. In November 1905 the upper seeds of 1904 burs stored in the laboratory, of 1904 burs buried eight months, and of 1905 burs gathered from the same patch, were removed and put to germinate. At 28–33°, with coats intact as Table VII shows, upper seeds of 1904 buried eight months gave 96 per cent. germination, upper seeds of 1904 stored in the laboratory gave 0 per cent., and upper seeds of 1905 gave 3 per cent. As shown in the same table, similar seeds with the coats removed in a germinator at 18–22° (near the minimum germinative temperature with the seed coats broken) gave in upper seeds of 1905 prompt germination, in upper seeds of 1904 stored

TABLE VII.

X. canadense; UPPER SEEDS.

Seeds	Coats	Temp.	Per cent. germinated after		
			3 days	6 days	33 days
1905 just gathered	on	28–33	0	0	3
1904 stored in laboratory 1 yr.	on	28–33	0	0	0
1904 in lab. 4 mos., buried 8 mos.	on	28–33	44	88	96
1905 just gathered	off	18–22	48	100	100
1904 stored in lab. 1 yr.	off	18–22	20	42	100
1904 in lab. 4 mos., buried 8 mos.	off	18–22	0	4	94

in the laboratory less prompt germination, in upper seeds of 1904 buried eight months much less prompt germination. From this table two things are evident. A period in the ground causes a partial disintegration of the seed coats which lowers the germinative minimum temperature with the seed coats intact. This accounts for the results in Table VII with the temperature at 28–33° and the coats intact. The vitality (if we mean by vitality the readiness with which seeds will germinate at a given temperature) of the embryos falls somewhat with a year of dry storage and markedly with eight months in the ground.

2. AXYRIS AMARANTHOIDES.

L. R. WALDRON of the North Dakota Agricultural College informed me that *Axyris amaranthoides* bears two kinds of seeds. One grows soon after being subjected to germinative conditions and the other fails to grow under similar conditions. The former, which is flattened and winged (*fig. 4, a*) he designated as *a*; the latter, which is almost spherical (*fig. 4, b*), as *b*. From material kindly furnished by him I have found that the distal portions of the branches bear entirely form *a*, and the proximal portions entirely form *b;* while the intermediate zone bears both forms even within the same seed cluster. Every seed is either one form or the other, there being no intergrading. Seeds of form *a* and *b* are about equal in number. It is found that form *b* fails to grow because the seed coat is only very slowly permeable to water. Form *a* soaked in water at 23°

FIG. 4.—Dimorphic seeds of *Axyris amaranthoides.*

absorbed after 24 hours 39 per cent. of dry weight, after 48 hours 70 per cent. Form *b* absorbed after 24 hours 4 per cent., after 48 hours 5 per cent., after 120 hours 6.5 per cent., and after 174 hours 9.5 per cent. After 174 hours soaking, 2 per cent. of form *b* had swollen up and germinated. At 23° with seed coats broken, as shown in Table IX, form *b* germinates much more readily than form *a* with seed coats intact, and somewhat more readily than form *a* with seed coats broken. It is evident from these tests that the embryo of form *b* is more vigorous than the embryos of form *a*.

It should be pointed out that the embryo of form *b* has an ideal storage condition. The water-excluding seed coat keeps it dry as it lies buried in the ground with the temperature relatively low. With the partial disintegration of the coat comes the admission of water and the growth of the embryo. The length of the delay in germination thus secured will vary greatly with water and temperature conditions, and with the different individuals of form *b*. It is probable that it will amount to many years in some cases.

In Axyris, as in the cocklebur, the same plant bears two sorts of seeds. One sort grows rapidly in nature and the other only after a considerable delay. Unlike the cocklebur, the seeds are not paired, and the delay is secured by the seed coat shutting out water rather than oxygen.

3. ABUTILON AVICENNAE AND CHENOPODIUM ALBUM.

Agriculturists claim that the seeds of *Abutilon Avicennae* lie in meadows and pastures for twenty years without growing, but upon breaking the soil grow in great abundance. When these seeds are soaked in water for forty-eight hours about 13 per cent. swell up, while the embryos of 87 per cent. remain extremely dry and can be pulverized. After weeks of soaking only a small per cent. additional will swell, a few at a time. For the relative per cent. of germination of these seeds with seed coats intact and seed coats broken see Table IX.

In *Chenopodium album*, mentioned in the NOBBE-HÄNLEIN table, about 16 per cent. of a crop of seeds swell up after twenty-four hours soaking. By continual soaking the remaining seeds gradually swell a few at a time, but much more readily than is the case with Abutilon.

Contrary to NOBBE AND HÄNLEIN's conclusion, the distributed germination shown by this species is secured by the slowness with which water penetrates the seed coats.

While in Axyris and Xanthium delayed or distributed germination is secured by peculiar seed coat characters of one form of the dimorphic seeds, in *Abutilon Avicennae* and *Chenopodium album* the distributed germination is secured by a variation in the seed coat characters of similar seeds.

4. IRIS.

Dr. C. J. CHAMBERLAIN informed me that he had never succeeded in germinating seeds of various species of Iris, although he had often attempted it in order to have root tips for cytological purposes. The bulk of the seed consists of the horny endosperm with food stored on the walls as hemicellulose. On one side of the endosperm is a cylindrical cavity in which the embryo is borne. The cavity is covered by a cap, thus entirely closing in the embryo. When the seed is dry, the embryo only partially fills the cavity, but after twenty-four hours soaking it completely fills it. In this condition, however, the seeds will lie for weeks without germinating. If now the caps are removed and the seeds still kept in the water, the embryo protrudes 3–7^{mm} within an hour. Seeds with caps removed germinate very readily, while those with caps intact do not germinate at all. For the effect of removing the cap in *Iris sibirica* and *I. Pseudacorus*, see Table IX. Increased oxygen pressure and high temperatures with the caps intact did not cause germination. With the caps removed, the most successful germination was secured by using sterilized sand as a germinator at 28–33°.

The amount of moisture absorbed by the embryo within the limiting wall of the endosperm is not sufficient to permit growth to begin. By taking away this limit to water absorption by removal of the cap or a portion of the endosperm in the region of the embryo, absorption is resumed and growth soon begins. Judging from a number of observations, it appears that in nature long soaking and accompanying disintegration lead to the loosening of the cap, or more frequently to the decay of the endosperm at one side of the embryo.

TABLE VIII.

SPECIES	TEMP. °C.	COATS	PER CENT. GERMINATED AFTER				
			2 days	3 days	5 days	9 days	38 days
Plantago major	28–33	entire	20	28	44	54	60
		broken	50	81	92	96	96
	18–22	entire	0	0	0	0	0
		broken	0	0	0	0	0
Plantago Rugelli	28–33	entire	2	2	9	15	38
		broken	91	98	98	98	98
	18–22	entire	0	0	0	0	0
		broken	0	0	0	12	12
Thlaspi arvense	28–33	entire	32	38	41	41	41
		broken	94	100	100	100	100
	18–22	entire	0	0	0	0	0
		broken	48	75	86	93	96

I was obliged to abandon work on these seeds, for on account of handling them I had repeated and severe attacks of dermatitis from contact with the syrupy covering of the endosperm. The symptoms were identical with those of Rhus poisoning.

5. THE NOBBE-HÄNLEIN TABLE.

Beside *Chenopodium album*, I have studied the following seeds mentioned in the NOBBE-HÄNLEIN table: *Aquilegia vulgaris, Capsella Bursa-pastoris, Lysimachia vulgaris, Plantago major, P. Rugelii,* and *Thlaspi arvense.* It was found, in agreement with NOBBE and HÄNLEIN, that all these seeds absorb water readily.

In *Aquilegia vulgaris* NOBBE and HÄNLEIN obtained a germination of only 0.75 per cent. after sixteen days, and no more during the remaining three years. In all tests at 23° I found over 50 per cent. germinating within thirty days. None generally germinated short of sixteen days because of the rudimentary state of the embryo. Breaking the seed coats cut down the percentage of germination by allowing infection by fungi which the slow growing embryos were unable to resist.

Table VIII shows the germination of seeds of *Plantago major, P. Rugelii,* and *Thlaspi arvense* at 18–22° and 28–33° with seed intact and seed coats broken. It is seen that with seed coats broken and with favorable temperatures over 95 per cent. germinate in every case. These results should be compared with Table I, in which

NOBBE and HÄNLEIN show the germination of only 0.25 per cent. of *P. major*, 10.75 per cent. of *P. media*, and 21.75 per cent. of *Thlaspi arvense* after 1,173 days. In the last species the germination is late in that period.

From Table VIII several important facts are evident. The temperature of 18–22° is below the minimum germinative temperature of seeds of *P. major* with seed coats intact or broken, and below that of *P. Rugelii* and *Thlaspi arvense* with seed coats intact. It is very near the germination minimum of *P. Rugelii* with seed coats broken and well above that of *Thlaspi arvense* in similar condition. A very marked increase in germination is secured by rupturing the coats even when the most favorable temperatures are used. High temperatures, then, will overcome only in part the seed coat effects. High temperatures are more efficient in overcoming the seed coat effects in *P. major* than in *P. Rugelii.*

In Table IX a similar effect of rupturing the seed coat is shown for *Capsella Bursa-pastoris*, *Lysimachia vulgaris*, and *Euphorbia Cyparissias*. It should be mentioned that the region and extent

TABLE IX.

TEMP. 18–22° EXCEPT FOR IRIS, WHICH WAS 28–33°.

SPECIES	COATS	PER CENT. GERMINATED AFTER					
		1 day	3 days	6 days	14 days	20 days	30 days
Abutilon Avicennae	entire	0	13	13	13	13	13
	broken	48	98	98	98	98	98
Avena fatua	entire	0	0	8	8	8	8
	broken	0	4	92	96	96	96
Capsella Bursa-pastoris	entire	0	8	14	15	15	15
	broken	0	80	100	100	100	100
Chenopodium album	entire	0	10	16	16	16	16
	broken	0	80	100	100	100	100
Euphorbia Cyparissias	entire	0	0	2	20	20	20
	broken	0	20	84	84	84	84
Lysimachia vulgaris	entire	0	0	0	0	0	0
	broken	0	44	60	64	64	64
Axyris amaranthoides A	entire	0	76	92	94	96	96
	broken	14	100	100	100	100	100
A. amaranthoides B	entire	0	0	0	0	0	0
	broken	55	100	100	100	100	100
Iris sibirica	cap on	0	0	0	0	0	0
	cap off	0	6	18	75	98	98
Iris Pseudacorus	cap on	0	0	0	0	0	0
	cap off	0	14	32	87	97	97

of the rupture makes no difference so long as the embryo is not injured.

Nobbe and Hänlein make no mention of the temperature maintained in the course of their experiments and seem unconscious of the fact that the temperature plays an important part. Judging from the results in Table VIII as compared with their results in Table I, they must have run their germinators at relatively low temperatures. These investigators, as well as Winkler, were likewise entirely unaware of the effect of the seed coats upon germination.

6. AVENA FATUA.

Avena fatua has some germinative characters which are interesting and which show that the seed coat characters just described for other seeds appear in the grasses. Table IX shows that at 18–22°, 8 per cent. grow with seed coats entire and 96 per cent. with coats broken. At 33°, 50–60 per cent. grow with coats entire and 97 per cent. with the coats broken. This seed coat character probably distributes the germination of a given crop over a period of years. It probably accounts for the claim of farmers that these grains will lie in pastures and meadows for twelve to fifteen years and then grow abundantly when land is plowed. Waldron (**12**) believes this idea is wrong, but it is easy to see how his vitality tests might be entirely misleading, for the seed coat character just described was not taken into account.

7. HAWTHORNS.

I found, as is popularly believed, that no hawthorn seeds will grow immediately after ripening. The seeds of various species were tested by removal of seed coats and subjection to high temperatures and high oxygen pressures; but none of these conditions sufficed to cause germination. Seeds that lay in the soil for a year or more germinated to some extent; while seeds stored in the dry for a similar period did not germinate at all, although the tests were made with naked embryos as well as with seeds bearing the coats. It is evident, therefore, that the change that must precede germination is in the embryo itself rather than in the seed coat; but it is also more or less a matter of disintegration, as is true in seeds whose germination is delayed by seed coats.

IV. General considerations.

Two statements of ARTHUR concerning the cocklebur need special consideration. He says: "Seeds in the bur retain their germinative power, when kept in a dry room, for two years or more; but seeds removed from the bur dry out within a few days and will no longer grow. Seeds removed from the bur and placed in a germinator retain their bright polished appearance as long as they are alive; when dead they turn dull and lusterless." I find that the seeds retain their vitality fully as well when removed from the bur and allowed to dry as when in the bur. In fact, a dry cool place is the best for storage of these seeds whether in or out of the bur, as is true for most seeds. The seeds removed from the bur and kept in a dry place retain their vitality much more than five years. I found the condition of the seed coat no indicator of the vitality of the embryo. The coat through disintegration loses its luster and turns black or sometimes colorless, which means that more oxygen is admitted and that the minimum germinative temperature of the seed has fallen. It is not surprising that ARTHUR drew these conclusions, for his work gave him no idea of the germinative conditions of the upper seeds or of the significance of the seed coat.

As DUVEL (**3***a*) states, seeds retain their vitality longest in conditions that permit of least respiration. KOLKWITZ (**5**) has shown that respiration is extremely slight in dry seeds at low temperatures. The embryos of seeds whose germination is delayed by coats that exclude oxygen, such as Abutilon, Axyris, and Chenopodium, are kept very dry by the coats. As they lie in the ground they are likewise relatively cool. In nature, in short, they have the most favorable storage conditions up to the time when the coats, through partial decay or long exposure to water, admit moisture and germination begins. It is not wonderful that such seeds lie in the ground twenty to twenty-five years and yet retain their vitality. While the reduction in the oxygen admitted to the upper seed of the cocklebur cuts down the respiration considerably, it does it to no such extent as does the exclusion of water. The coats that exclude water are undoubtedly much better adapted to securing a long delay than are the coats that merely exclude oxygen. In nature the longer delays are certainly secured by the former method.

PFEFFER (**9**) says: "The conditions which lead to certain seeds resting under the soil for as long as fifty years and germinating when dug up have not as yet been determined." This, as well as the sudden appearance of weeds in forests after fires and in meadows of many years standing immediately upon plowing, is probably explained by a few simple facts. Weed seeds are produced in great abundance. Because of variation in seed coat characters or in some cases of embryo characters, a given crop distributes its germination over a period of years. Seeds deep in the soil germinate less readily because of lack of oxygen or water, and those that do grow exhaust the stored food before reaching the surface. Bringing such seeds to the surface greatly increases their germination and removes the danger of exhaustion of the stored food. The plants of meadows and forests keep the water supply reduced and thereby cut down the chances for the germination and later growth of the weed seeds present. With the destruction of the plants of the forest or meadow comes a great increase in the germination of the weed seeds and a removal of the opposition to their future growth. These phenomena, then, will probably all be explained by a study of the germinative characters of the seeds such as is described in the experimental portion of this paper, along with certain other well established facts on germination.

It is undoubtedly true that many of the tests that have been made for the vitality of weed seeds are untrustworthy, because the significance of the seed coats has been overlooked. This is clearly shown by the results of DUVEL (**3***b*) and WALDRON (**12**), who have carried on extensive experiments to determine the length of time weed seeds must be buried in order to lose their vitality. In column I of Table X is shown the percentage germination determined by me with seed coats broken and with favorable temperatures. In column II appear DUVEL's results, in which he uses what he terms the "most favorable temperatures," but overlooks of course the seed coat effects. The figures quoted from DUVEL are from the column "original samples," which means fresh seeds, as were the seeds for determining the percentages of column I.

The effect of rupturing the seed coats, as is shown in this table, is very evident, although DUVEL has in part overcome the seed coat effects by high temperatures. The average percentage of germina-

TABLE X.

	I	II
1. Axyris amaranthoides	100	0
2. Xanthium pennsylvanicum	98	50
3. Thalaspi arvense	100	57
4. Plantago Rugelii	96	4
5. Avena fatua	96	75
6. Plantago major	96	24
7. Chenopodium album	100	67

tion for the seven species tested is 98 per cent. with seed coats ruptured, 40 per cent. with seed coats intact. It may be urged that the seeds used by DUVEL are of low vitality. This, however, does not seem at all probable, for I obtained only slightly higher percentages, as shown in Tables VIII and IX, with the coats intact and with favorable temperatures, than those reported by DUVEL. These slightly higher percentages can be accounted for by the fact that the temperature used by me was 28–33°, while the temperature used by DUVEL was 20–30°. Two species of seeds mentioned in this table need special consideration. In *Axyris amaranthoides*, DUVEL determined the vitality as 0 per cent. This is exactly what would be expected if form *b* alone (as shown in Table IX) were used, and if the effect of the seed coat were overlooked. In *Xanthium pennsylvanicum* he finds 50 per cent. germinating. This, too, is what would be expected if the upper and lower seeds of the cocklebur were put in a germinator at 20–30°. The lower seeds would germinate in this condition and the others fail to do so. It seems probable, then, that in Xanthium and Axyris DUVEL overlooked the dimorphic character of the seeds, as well as the effect of the coats on germination. Vitality tests of this kind, that neglect the effect of the seed coats, are tests of the condition of the seed coats rather than tests of the real vitality of the embryos themselves. It is evident that if these errors appear in the original tests for vitality they will likewise appear in the tests made after different periods of burial. If vitality tests, looking to the extermination of weeds, are to be of real value, the exact germinative character of each species must first be determined, and all vitality tests must then be made on the basis of these germinative characters.

It is obvious that the seeds which fail to grow in the ordinary grain tests often do so because of seed coat characters rather than because of lack of vitality of the embryos. This, however, does not in any wise invalidate the ordinary methods of testing grains to be used for seeding, since seeds that are delayed a month or more in germination are of no value in producing the crop. On the other hand, when it comes to testing weed seeds, looking toward extermination, it is highly important that these seed coat characters be taken into consideration.

I am impressed by the high vitality of weed seeds. This is especially true of the more noxious weeds and those in which the seed coat secures a long delay. The high vitality is not shown alone by a quick response to germinative conditions. The percentage of germination in noxious weeds, provided real germinative conditions are given (the seed coat hindrance removed), is very close to 100; and a marked growth of the embryo generally takes place within two days after being subjected to germinative conditions. After recognizing this fact, one is led to suspect that many other cases of low vitality in weed seeds mentioned by DUVEL and others (not examined in this paper) must be due to seed coat characters rather than to lack of vitality in the embryos.

While this paper indicates, exactly contrary to the conclusions commonly held, that delayed germination is in most cases secured by seed coat characters, it yet recognizes that in the hawthorns delay is secured by embryo characters. It is probable that a number of other seeds will be found to belong to the same category as the hawthorn. It is of great interest to know just the changes which take place in the seeds of the hawthorns and finally lead to germination through long exposure to germinative conditions. This subject is now under investigation. It must be urged that, until these changes are understood, any attempt to determine the vitality of such seeds is futile.

The methods by which seed characters that secure delayed germination have come about naturally deserves consideration. It may be adaptation coming through natural selection, but an attempt to prove this would end in failure. This delay in many cases, however, is of undoubted advantage to the species. ARTHUR urges that in the cocklebur the two seeds are borne in an indehiscent structure, the bur, and that it is impossible to have the two seeds distributed in space, so a distribution in time is substituted. Why such an indehiscent involucral structure should be developed instead of such a bur as appears in the burdock needs answer. With the indehiscent bur already in existence the advantage is plain. It is clear that such germinative characters as appear in the seeds of *Axyris amaranthoides*, *Abutilon Avicennae*, etc., insure that the soil will always be supplied with these seeds in process of germination. The destruction of existing vegetation, by fire or otherwise, is followed by a quick appearance of these weeds. In species where none of a given crop of seeds grow until a year or more after falling, it would seem that the adaptive characters, if they be such at all, had overstepped the line of greatest advantage.

V. Summary.

1. Delayed germination is reported in the seeds of many plants and, exactly opposite to the common view, its cause generally lies in the seed coats rather than in the embryos; but in the hawthorns, as perhaps in some other seeds, it is due to embryo characters.

2. In the upper seed of the cocklebur the delay is secured by the seed coat excluding oxygen, while in *Axyris amaranthoides*, *Abutilon Avicennae*, and many other seeds, it is secured by the coats excluding water.

3. In Iris seeds the failure to germinate is due to the endosperm and cap stopping water absorption before the quantity necessary for germination is obtained by the embryo.

4. In *Plantago major*, *P. Rugelii*, *Thlaspi arvense*, *Avena fatua*, and others, the real method by which the coats secure the delay is not yet determined, but there is no doubt that the delay is due to the coats.

5. Seed coats which exclude water are much better adapted to securing delays than are seed coats which exclude oxygen, because of the much greater reduction of respiration in the first case.

6. In nature growth of the delayed seeds comes about through the disintegration of the seed coat structures by a longer or shorter exposure to germinative conditions, and the length of the delay depends upon the persistence of the structure securing it.

7. In the cocklebur the bur aids in preserving the seed coat of the upper seed by being most persistent over it.

8. Even in the hawthorns, where the delay is secured by embryo characters, the germination finally comes about in the course of long exposure to germinative conditions and not in dry storage.

9. In the cocklebur the seed coats of both the upper and lower seeds cut down the oxygen supply, but the first the more markedly. This gives the upper seed a much higher minimum germinative temperature and the lower seed a somewhat higher one. Hence we have in the cocklebur seeds two minimum germinative temperatures; one with the seed coats intact and a much lower one with the coats removed. In the upper seeds these differ by fifteen or more degrees; in the lower seeds by three to five degrees.

10. High temperatures bring about the germination of the upper seeds of the cocklebur with coats intact by increasing the rate of diffusion of oxygen through the seed coat and by raising the respiratory ratio.

11. The minimum germinative temperatures of the seeds of the cocklebur, *Plantago major*, *P. Rugelii*, *Thlaspi arvense*, and various other seeds, with the seed coats intact, is far above the highest minimum germinative temperature reported; while in the cocklebur and *Plantago major* with coats removed this critical temperature is considerably above the highest reported.

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LITERATURE CITED.

1. ARTHUR, J. C., Delayed germination in the cocklebur and other paired seeds. Proc. Soc. Prom. Agric. Science **16**:70–79. 1895.

2. DETMER, W., Keimungsprocess der Samen 427. 1880.

3*a*. DUVEL, J. W. T., Vitality and germination of seeds. U. S. Dept. Agric., Bur. Plant Ind., Bull. 58. 1904.

3*b*. ———, Vitality of buried seeds. Idem, Bull. 83. 1905.

4. KIENITZ, M., Ueber Ausführung von Keimproben. Bot. Centralbl. **1**:52–53 1880.

5. Kolkwitz, R., Ueber die Athmung ruhenden Samen. Ber. Deutsch. Bot. Gesells. **19**:285–287. 1901.

6. Kuntze, Richard E., Germination and vitality of seeds. Published by the Torrey Bot. Club. 1901.

7. Masterman, E. E., Sprouting of cocklebur seeds. Ohio Nat. **1**:69–70. 1901.

8*a*. Nobbe, F., and Hänlein, H., Ueber dei Resistenz von Samen gegen die aüsseren Factoren der Keimong. Landw. Versuchs-Stat. **20**:63–96. 1877.

8*b*. ———, Ueber die Keimkraft von Unkrautsamen. Landw. Versuchs-Stat. **25**:465–470. 1880.

9. Pfeffer, W., Physiology of plants (Eng. ed.) **2**:208. 1900.

10. Stone, G. E., Influence of chemical solutions upon the germination of seeds. Rept. Mass. Agr. Exp. Sta. **13**:74–83. 1901.

11. Thompson, A., Zum Verhalten alter Samen gegen Fermentlösung. Gartenflora **45**:344. 1896.

12. Waldron, L. R., Buried weed seeds. N. Dak. Agr. College Bull. 62. 1904.

13. Waugh, Frank A., The enzymic ferments in plant physiology. Science N. S. **6**:950–952. 1897.

14. Wiesner, J., Ueber die Ruheperiode und von einige Keimungsbedingungen der Samen von *Viscum album*. Ber. Deutsch Bot. Gesells. **15**:503–515. 1897.

15. Winkler, A., Bermerkungen über die Keimpflanzen und die Keimfähigkeit des Samen von *Tithymalus Cyparissias*. Ber. Deutsch. Bot. Gesells. **1**:452–455. 1883.

UNDESCRIBED PLANTS FROM GUATEMALA AND OTHER CENTRAL AMERICAN REPUBLICS. XXVIII.[1]

JOHN DONNELL SMITH.

Saurauja Maxoni Donn. Sm.—Glaberrima. Folia nitida obovato-oblonga in apicem angulo obtuso in basin angulo acuto desinentia calloso-denticulata, nervis lateralibus remotissimis arcuatis. Paniculae subterminales longe pedunculatae folia subaequantes. Sepala paene glabra.

Frutex 3–4-metralis, ramulis laevibus. Folia crassa $14–20^{cm}$ longa $6–8^{cm}$ lata, margine vix ac ne vix undulato, nervis lateralibus haud parallelis $1.5–2^{cm}$ inter se distantibus, petiolis validis $2–3^{cm}$ longis. Pedunculi $10–17^{cm}$ longi et panicularum axes complanati striati nitidi, axibus primariis alternis $1.5–2.5^{cm}$ longis, pedicellis $4–5^{mm}$ longis, bracteis linearibus 4^{mm} longis et bracteolis ciliolatis, floribus 2.5^{cm}-diametralibus. Sepala ovalia $7–8^{mm}$ longa juxta marginem basinque intus pubescentia. Petala discreta oblongo-ovata bilobulata. Filamenta basi cinereo-barbata antheris aequilonga, loculis dimidio discretis. Ovarium glabrum 5- vel rarius 3-loculare, stylis discretis 4.5^{mm} longis.

Secanquim, Depart. Alta Verapaz, Guatemala, alt. 550^{m}, Jan. 1905, *Maxon et Hay* (n. 3221).

Saurauja ovalifolia Donn. Sm.—Strigillosa. Folia ovalia bis longiora quam latiora apice obtusa basi rotundata supra scabriuscula subtus nervatione pubescentia mucronulis denticulata. Paniculae pauciflorae. Sepala strigillosa et pubescentia. Bacca magna villosa.

Frutex orgyalis. Ramuli petioli pedunculi panicularum axes strigillis ferrugineis pilo albo apiculatis operti. Folia $20–23^{cm}$ longa, nervis lateralibus utrinsecus 20–22, venis utrinque manifestis, petiolis circiter 2.5^{cm} longis. Pedunculi ex quaque axilla nascentes $7–10^{cm}$ longi, paniculis $4–6^{cm}$ longis, axibus plerumque geminatis $1–2^{cm}$ longis, pedicellis $5–10^{mm}$ longis, bracteolis linearibus $7–10^{mm}$ longis. Sepala acuminato-ovata 7^{mm} longa. Bacca sordide villosa 9^{mm}-diametralis 5-locularis polysperma, stylis discretis 5^{mm} longis, seminibus obovatis scrobiculatis.—Petala et stamina in exemplis suppetentibus deficiunt. Río Navarro, Prov. Cartago, Costa Rica, alt. 1100^{m}, Mart. 1894, *J. Donnell Smith*, n. 4746 ex Pl. Guat. etc. quas ed. Donn. Sm.

Saurauja subalpina Donn. Sm.—Furfuraceo-strigillosa. Folia longe petiolata oblanceolata utrinque acuta mucronulis incurvis

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[1] Continued from BOT. GAZETTE 40:11. 1905.

denticulata supra tuberculis rubiginosis setuligeris scabra subtus nervis approximatis et venis rufo-strigillosa et parce pubescentia. Pedunculi petiolis parum longiores, floribus inter majores. Sepala furfuracea tuberculato-setulosa. Ovarium glabrum.

Ramuli petioli pedunculi panicularum axes simul cano-furfuracei et longe rufo-strigillosi. Folia 20–22^{cm} longa 6–7^{cm} lata, nervis 5–8^{mm} inter se distantibus, venis minutissime reticulatis subtus tantum manifestis, petiolis 3–4^{cm} longis. Pedunculi axillares 4–5^{cm} longi, paniculis circiter 6^{cm} longis floribundis, axibus alternis, pedicellis 4–8^{mm} longis, bracteolis linearibus 3–5^{mm} longis, floribus 2.5^{cm}-diametralibus. Sepala ovata 6–8^{mm} longa, setulis validis brevibus puberulis. Petala discreta obovato-oblonga. Filamenta pilis articulatis barbata antheris infra medium affixis paulo longiora, loculis triente discretis. Ovarium 4–5-loculare stylis discretis 6^{mm} longis bis superatum.

Volcán de Agua, Depart. Zacatepéquez, Guatemala, alt. 3300^{m}, Apr. 1890, *J. Donnell Smith*, n. 2171 ex Pl. Guat. &c. quas ed. Donn. Sm.

PRUNUS CAPOLLIN Zucc., var. **prophyllosa** Donn. Sm.—Ramuli racemiferi peruliferi subaphylli pedunculum lateralem mentientes, perulis ovalibus 12–18^{mm} longis apice retusis sicut stipulae lineari-lanceolatae glandulo-denticulatae 16–19^{mm} longae atque bracteolae oblongae 7–10^{mm} longae purpurascentibus pubescentibus. Flores nondum satis evoluti solum cogniti.

San Rafael, Depart. Zacatepéquez, Guatemala, Mart. 1905, *Maxon et Hay* (n. 3666).

Tibouchina paludicola Donn. Sm. (§ DIOTANTHERA Triana.)—Patentim glandulari-setulosa. Folia ovata vel lanceolato-ovata acuminata basi rotunda vel leviter cordata supra sparse, subtus nervis venisque, setulifera denticulata 7–9-nervia. Flores axillares singuli vel cymulis trifloris terminales. Stamina glaberrima cum staminodiis alternantia, connectivo longe producto. Ovarium nudum.

Rami subteretes fistulosi et petioli pedicelli calyces setulis patulis glanduliferis conspersi. Folia membranacea 4–8^{cm} longa 2–4^{cm} lata subtus minutius setulifera, petiolis 1–1.5^{cm} longis. Cymulae semel bisve trichotomae foliaceo-bracteolosae, pedicellis lateralibus 5^{mm} longis, dichotomali brevissimo. Calycis setulae purpureae, tubus oblongo-campanulatus 5–6^{mm} longus segmenta attenuato-linearia subaequans. Stamina 5 subaequalia 16–17^{mm} longa, antherarum tubo apicali 2^{mm} longo, connectivo usque ad 3.5^{mm} producto. Staminodia filiformia 4^{mm} longa ananthera. Ovarium ovoideum 3^{mm} altum vertice nec hispidum nec setosum, stylo 2^{cm} longo. Fructus globoso-ovalis 8^{mm} longus.—Species staminodiis et ovario anomala.

In paludibus secus Río Cañas Gordas, Comarca de Puntarenas, Costa Rica, alt. 1100^{m}, Mart. 1897, *Pittier* (nn. 11055, 11056).—In filictis paludosis secus Río El General, Diquis, Comarca de Puntarenas, C. R., alt. 700^{m}, Febr. 1898, *Pittier* (n. 12150).

Monolena Guatemalensis Donn. Sm.—Rhizoma glabrum elongatum. Folia longe petiolata cordato-ovata acuminata integra 7–9-plinervia, lobis basalibus imbricatis. Scapus basi squamis fultus ceterum nudus petiolo longior pluriflorus. Styli basis ovoidea quam capsula major.

Rhizoma $8–17^{mm}$ crassum 7^{cm} et ultra longum fibrillosum squamis triangularibus 1^{mm} longis ferrugineis conspersum, squamis scapum fulcientibus imbricatis triangularibus vel lanceolatis $3–7^{mm}$ longis. Folia ob folium alterum caducum quasi alterna $10–16^{cm}$ longa $6–10^{cm}$ lata utrinque punctulata et lineolata mucrunculis hinc inde ciliata, petiolis $6–19^{cm}$ longis. Scapus $14–20^{cm}$ longus sicut petiolus in sicco rubescens, cyma 4–8-flora, pedicellis $2–3^{mm}$ longis, bracteis caducis. Calycis florentis tubus carnosulus 3^{mm} altus, lobi membranacei ovati 1.5^{mm} longi. Calycis fructiferi aucti 5^{mm} alti latera 11^{mm} longa cartilaginea pallida reticulato-nervosa exlobata. Petala 23^{mm} longa rosea. Capsula calyce 3-plo superata, valvis acute triangularibus 3^{mm} longis sicut styli basis 4^{mm} longa cartilagineis pallidis, seminibus vix 1^{mm} longis.

Guatemala, Depart. Alta Verapaz: in fundo *Sepacuité* dicto, Mart. 1902, *Cook et Griggs* (n. 106), Apr. 1902, *Cook et Griggs* (n. 575); in declivibus humidis inter Senahú at Actalá, Jan. 1905, *Maxon et Hay* (n. 3331); secus viam inter Sepacuité et Secanquim, alt. 1200^{m}, Maj. 1905, *H. Pittier* (n. 314).

Conostegia dolichostylis Donn. Sm.—Tota praeter foliorum paginam superiorem plus minus dense stellato- et ferrugineo-pubescens. Folia lanceolata superne subsensim tenuiterque, deorsum brevius, acuminata obsolete sinuato-denticulata 5-plinervia. Flores pauci graciliter pedicellati 5-meri inter maximos. Stylus stamina longe superans.

Ramuli teretes et petioli dense pubescentes. Folia membranacea $8–15^{cm}$ longa $3–5^{cm}$ lata leviter disparia supra glabra subtus nervis venisque pubescentia et demum inter nervos glabrescentia, nervo utroque superiore $10–22^{mm}$ supra basin limbi prodeunte, petiolis $1–3^{cm}$ longis. Panicula in exemplo unico manco suppetente 3-flora ut videtur, pedunculo 5^{mm} longo, pedicellis 11^{mm} longis. Calycis tubus turbinato-campanulatus 7^{mm} longus atque latus pubescens. Petala obovata 12^{mm} longa. Antherae crasso-oblongae 5.5^{mm} longae filamenta aequantes. Stylus 15^{mm} longus, stigmate hemispherico 1^{mm}-diametrali. Alabastra ignota.—*C. arboreae* Schauer proxima.

In silvis ad Buenos Aires, Comarca de Puntarenas, Costa Rica, Febr. 1892, *Tonduz* (n. 4943).

Conostegia rhodopetala Donn. Sm.—Folia glabra coriacea oblongo-lanceolata caudato-acuminata basi acuta integra triplinervia. Panicula pyramidata decomposita, axibus primariis 4-verticellatis. Calycis tubus campanulatus limbus conicus rostratus. Petala obovato-orbicularia.

Arbor, ramulis obtuse tetragonis, junioribus uti folia nascentia et panicula leviter furfuraceis. Folia decussata in eodem jugo satis inaequalia 15–20$^{\mathrm{cm}}$ longa 5–8$^{\mathrm{cm}}$ lata in caudam linearem 8–10$^{\mathrm{mm}}$ longam desinentia, nervis paulo supra basin egredientibus validis, duobus basalibus submarginalibus tenuibus interdum adjectis, venis transversis 4–6$^{\mathrm{mm}}$ inter se distantibus, petiolis 2–5$^{\mathrm{cm}}$ longis. Panicula 15–20$^{\mathrm{cm}}$ alta densiflora, pedicellis 7–12$^{\mathrm{mm}}$ longis, floribus 6-meris. Alabastra rostello 2–3$^{\mathrm{mm}}$ longo adjecto 9$^{\mathrm{mm}}$ longa 3$^{\mathrm{mm}}$ crassa. Petala 6$^{\mathrm{mm}}$ longa rosea. Stamina 12–14, antheris leviter arcuatis. Stylus 4$^{\mathrm{mm}}$ longus crassus, stigmate capitato.—Juxta methodum in Monographia clari COGNIAUX expositam apud *C. Pittieri* Cogn. collocari debet.

In sylvis ad La Palma, Prov. San José, Costa Rica, alt. 1500–1800$^{\mathrm{m}}$, Jul. 1895, *Tonduz* (n. 9702), Sept. 1896, *Pittier* (n. 10169), Maj. 1898, *Tonduz* (n. 12347).—Las Lajas, San Isidro, Prov. Heredia, Costa Rica, alt. 1500$^{\mathrm{m}}$, Sept. 1900, *Pittier* (n. 14022).

Conostegia vulcanicola Donn. Sm.—Stellulato-pubescens. Folia supra glabrescentia subtus nervis venisque pubescentia lanceolato-elliptica utrinque acuminata margine setulifera quintuplinervia, nervis superioribus a basi remotis. Alabastra inter minima oblongo-ovoidea medio constricta superne conica apiculata. Flores 5–6-meri.

Ramuli teretes. Folia nascentia utrinque ferrugineo-tomentulosa, provectiora supra pilosiuscula vel glabrescentia subcoriacea 8–14$^{\mathrm{cm}}$ longa 3–5.5$^{\mathrm{cm}}$ lata in eodem jugo parum aequalia apice curvilineo-acuminata, nervis superioribus 1.5–2.5$^{\mathrm{cm}}$ supra basin limbi a medio secendentibus, setulis marginalibus cito caducis, petiolis tomentulosis 1.5–2.5$^{\mathrm{cm}}$ longis. Panicula pyramidalis trichotoma pubescens, pedicellis 1–3$^{\mathrm{mm}}$ longis. Alabastra 5–6$^{\mathrm{mm}}$ longa 3$^{\mathrm{mm}}$ crassa exrostrata basi subtruncata pube punctulata vel glabrescentia. Petala obovata 5$^{\mathrm{mm}}$ longa crenulata flava. Stamina 10–12, antheris rectis 2$^{\mathrm{mm}}$ longis. Stylus 4$^{\mathrm{mm}}$ longus, stigmate non dilatato. Fructus urceolato-globularis 4$^{\mathrm{mm}}$ diametralis glabrescens in sicco plumbeus.—Ad *C. Cooperi* Cogn. quibusdam notis accedens foliorum nervatione recedit.

In silvis ad Achiote in monte vulcanico *Poás* dicto, Prov. Alajuela, Costa Rica, alt. 2200$^{\mathrm{m}}$, Nov. 1896, *Tonduz* (nn. 10836, 10840).

Miconia astroplocama Donn. Sm. (§ TAMONEA Cogn.)—Pilis stellatis luteo-fuscis tomentulosa. Folia supra nitida subtus praesertim ad nervos pilosa lanceolato-oblonga apice longe acuminata basi acutiuscula valde disparia 5-nervia. Flores pedicellati terni 5-meri. Calyx lobatus petalis dimidio longior. Filamenta glabra, antheris profundiuscule bilobatis.

Arbor, coma rotundata, ramulis teretibus et petiolis panicula calycibus dense tomentulosis. Folia subcoriacea integra supra glabra et in herbario nigricantia subtus inter nervos pilis e papilla ferruginea pluriradiatis conspersa, cujusque paris folio altero 18–33^{cm} longa 5–12^{cm} lato quam minus breviter petiolatum 2–3-plo majore, petiolis crassis 2–5.5^{cm} longis. Panicula pyramidalis foliis brevior multiflora, cymulis trifloris, pedicellis 2–4^{mm} longis. Calyx anguste campanularis 4.5^{mm} longus limbo haud dilatato 2^{mm} latus, lobis parvis rotundatis extus tuberculo punctatis. Petala quadrato-oblonga 3^{mm} longa. Antherae lineares inaequales 3–4^{mm} longae incurvae fere usque ad 0.5^{mm} supra basin affixae. Ovarium semiliberum 3-loculare, stylo 9^{mm} longo. Bacca globosa 5^{mm} diametralis stellato pilosa.

In silvis ad fundum *Tuís* vocatum, Prov. Cartago, Costa Rica, alt. 650^{m}, Nov. 1897, *Tonduz* (n. 11438).—In silvis ad Las Vueltas, Tucurrique, Costa Rica, alt. 700^{m}, Dec. 1898, *Tonduz* (n. 12872).

Miconia nutans Donn. Sm. (§ LACERARIA Naud.)—Leviter furfuracea. Folia supra glabra subtus praetermissis nervis glabrescentia obovato-oblonga cordato-acuminata in petiolum canaliculatum attenuata subobsolete sinuato-denticulata 5-plinervia, venis transversalibus crebris. Flores 5-meri. Calyx medio constrictus. Petala lineari-oblonga. Ovarium 5-loculare.

Ramuli obtuse tetragoni et petioli panicula foliorum subtus nervi furfuribus minutis glandularibus stellatis ferruginosi. Folia coriacea siccitate utrinque laete viridia subtus primum furfuracea demum inter nervos furfurium reliquis rubro-punctulata satis disparia 15–25^{cm} longa 7–10^{cm} lata, nervo utroque superiore circiter 5^{mm} supra basin limbi a medio secedente, inferiore submarginali, venis transversalibus angulo recto patulis simplicibus 3–5^{mm} inter se distantibus subtus conspicuis, petiolis 2–3^{cm} longis. Paniculae singulae vel ternae pyramidales foliis superatae apice nutantes repetitus-trichotomae, floribus sessilibus vel breviter pedicellatis, bracteolis oblongis cito caducis. Calyx pallide furfuraceus 3.5^{mm} longus, tubo subgloboso, limbo dilatato 2.5^{mm} lato usque ad medium in lobos ovatos disrupto. Petala 4^{mm} longa 1^{mm} lata utrinque truncata nervata. Antherae vix 3^{mm} longae. Ovarium fere totum adnatum, stylo 7–8^{mm} longo. Bacca depresso-globosa 3^{mm} alta 4.5^{mm} crassa 10-costata limbo 2^{mm} alto coronata.—*M. aureoidi* Cogn. proxima.

Comarca de Puntarenas, Costa Rica, alt. 1100^{m}, Febr. 1897, *Pittier*, ad ripas Río Coto (n. 11059), in paludosis secus Río Cañas Gordas (n. 11060).—In fundo *Cubilquitz* dicto, Depart. Alta Verapaz, Guatemala, alt. 350^{m}, Oct. 1903, *von Tuerckheim*, n. 8522 ex Pl. Guat. &c., quas ed. Donn. Sm. Sub *M. obovali* Naud. olim distributa.

Blakea anomala Donn. Sm.—Folia obovato-elliptica abrupte caudato-acuminata basi acuta quinquenervia breviter petiolata. Pedunculi solitarii filiformes. Bracteae exiguae triangulares. Calyx primum clausus deinde in lobos 4 tubum aequantes dirumpens.

Saprogena. Rami teretes, ramulis petiolisque dense paleaceo-furfuraceis. Folia chartacea supra glabra subtus nervis leviter furfuracea in eodem jugo satis inaequalia consimilia 5.5–10^{cm} longa 3–5.5^{cm} lata in caudam 1–1.5^{cm} longam desinentia, venis transversis 0.5–1^{mm} inter se distantibus, petiolis 5–8^{mm} longis. Pedunculi leviter furfuracei 3–6^{cm} longi, bracteis 1.5–2.5^{mm} longis inaequalibus basi connatis, alabastris turbinatis, floribus praetermisso calyce 6-meris. Calyx coloratus cum bracteis tenuissime furfuraceus, tubo campanulato 7^{mm} longo totidemque lato, lobis deltoideo-ovatis intus densius furfuraceis. Petala obovato-oblonga 14–15^{mm} longa. Antherae pendulae connatae ovales filamentis rubris 6^{mm} longis bis superatae, calcare acuto. Stylus 7^{mm} longus.—Ad *B. gracilem* Hemsl. habitu accedens ab omnibus congeneribus bracteis necnon calyce insigniter recedit.

In truncis putridis ad La Palma, Prov. San José, Costa Rica, alt. 1450–1550^{m}, Sept. 1896, *Pittier* (n. 10165), Sept. 1898, *Tonduz* (n. 12521).

Passiflora Salvadorensis Donn. Sm. (§ EUDECALOBA Mast.)—Folia subtus glauca ima basi cuneata paulo infra medium biloba, lobis divergentibus paulo longioribus quam latioribus rotundatis. Pedunculi petiolos subaequantes. Calyx basi patelliformis, segmentis linearibus pedunculo bis terve brevioribus. Coronae faucialis fila petalis aequilonga, corona basali 5-crenata. Gynophorum gracillimum. Filamenta sicut styli perelongata.

Scandens glabra, ramis angulatis. Folia circumscriptione quasi semiovata 8–9^{cm} longa 6.5–8.5^{cm} lata membranacea subtus inter nervos glandulis magnis ocellata trinervia, lobis et sinu vix lobulato nervo exeunte aristulatis, nervis lateralibus angulo semirecto divergentibus, petiolis eglandulosis 3–5^{cm} longis, stipulis filiformibus. Pedunculi 2–3-ni medio filiformi-bracteati, alabastris e basi truncata oblongis. Sepala 16^{mm} longa. Petala hyalina linearia 8^{mm} longa. Corona faucialis filamentosa, filis uniseriatis linearibus purpureis. Corona mediana late tubulosa 3–4^{mm} alta plicata denticulata purpurea. Corona basalis 1–2^{mm} alta herbacea. Gynophorum 12^{mm} longum. Filamenta stylos subaequantia 8–9^{mm} longa. Ovarium globoso-ovale 1^{mm} longum. Fructus ignotus. —*P. ornithourae* Mast. affinis. Ab incolis *Calzoncillos* facete dicitur.

San Salvador, Republ. del Salvador, Maj. 1905, *Luis V. Velasco*, n. 8887 ex Pl. Guat. &c. quas ed. Donn. Sm.

Dendropanax querceti Donn. Sm.—Folia breviter petiolata lanceolata apice curvilineo-acuminata infra medium sensim angustata calloso-denticulata. Umbella solitaria, pedunculo petiolis paulo longiore pedicellos vix superante ima basi bracteoso apice in receptaculum ferrugineo-bracteolosum dilatato.

Glabrum dichotomo-ramosum. Folia coriacea 5–10^{cm} longa 3–4-plo longiora quam latiora calloso-apiculata, nervis lateralibus utrinque 11–14, duobus infimis submarginalibus longius ascendentibus, reticulis minutis, petiolis 4–10^{mm} longis. Pedunculus robustus 6–12^{mm} longus, bracteis imbricatis scariosis ovatis mucronatis, receptaculi bracteolis paleaeformibus lanceolatis pulverulentis, umbella unica simplice 12–18-flora, pedicellis 5–10^{mm} longis. Calycis tubus obconicus 2^{mm} longus, margo mucronulis denticulatus. Petala ovata 1-nervia apice inflexa calycem aequantia. Stamina petalis aequilonga, antheris ovalibus. Discus a calyce angustissime liber. Styli in columnam connati. Fructus globosus 4–5^{mm}-diametralis.

In quercetis ad El Copey, Prov. Cartago, Costa Rica, alt. 1800^{m}, Mart. 1896, Mart. 1898, *Ad. Tonduz* (nn. 11826, 12196).

Rondeletia aetheocalymma Donn. Sm. (§ ARACHNOTHRYX Benth. et Hook.)—Glabra. Folia obovato-elliptica subabrupte acuminata basi acuta. Stipulae lineari-oblongae mucronulatae. Corymbus obpyramidalis trichotomo-cymosus, floribus pilosis. Calycis lobi elliptici, altero ceteris inaequalibus 2–3-plo majore quam tubus corollinus cylindricus bis breviore.

Frutex 3–4-metralis, ramis et foliis nitidis. Haec coriacea 12–15^{cm} longa 5–7^{cm} lata, nervis lateralibus utrinque 9–11, venulis subimmersis, petiolis 9–12^{mm} longis, stipulis 6–9^{mm} longis. Corymbus terminalis folia superans, pedunculo 4–11^{cm} longo, axibus semierectis pubescentibus, primariis foliaceo-bracteatis 3.5–5.5^{cm} longis, secundariis 1.5–2.5^{cm} longis, bracteolis linearibus 6–12^{mm} longis glabris, floribus tetrameris, dich[illegible], lateralibus brevissime pedicellatis. Calycis tubus cano-sericeus, lobi glabrescentes, maximo 7^{mm} longo 3^{mm} lato. Corollae albae tubus 13^{mm} longus cano-pilosus, os nudum exannulatum, lobi obovato-rotundi undulati intus farinosi. Capsula depresso globosa 6^{mm}-diametralis pilosa polysperma.—*R. linguiformi* Hemsl. proxima.

Secus viam inter Sepacuité et Secanquiḿ, Depart. Alta Verapaz, Guatemala, alt. 550–900^{m}, Jan. 1905, *Maxon et Hay* (n. 3275).

Rondeletia stachyoidea Donn. Sm. (§ ARACHNOTHRYX Benth. et Hook.)—Folia anguste lanceolata utrinque, praesertim sursum, attenuata supra parce pilosa subtus strigillosa. Thyrsus spiciformis, capitellis subsessilibus 2–3-floris. Calycis arachnoideo-pilosi lobi lineari-lanceolati paulo inaequales. Corolla praeter lobos extus basi barbatos glabra. Capsula parva.

Arbuscula quinquemetralis, ramulis appresse pilosis, internodiis, saltem superioribus, brevissimis. Folia 10–16^{cm} longa 2–3.5^{cm} lata sursum tenuissime acutissimeque attenuata supra cito glabrescentia, nervis lateralibus utrinsecus circiter 9 longe ascendentibus subtus conspicuis, petiolis 5–10^{mm} longis pilosis, stipulis lineari-lanceolatis filiforme attenuatis 1.5^{cm} longis internodia superiora aequantibus. Thyrsus terminalis 9–11^{cm} longus pilosus, bracteolis lineari-lanceolatis calycem aequantibus arachnoideo-pilosis, floribus subsessilibus tetrameris. Calycis lobi 3–4^{mm} longi. Corollae albae tubus tenuis 8^{mm} longus sursum leviter ampliatus, os nudum exannulatum, lobi rotundati. Capsula globosa 2^{mm}-diametralis pilosiuscula polysperma.—*R. gracili* Hemsl. affinis differt inter alia capitellis paene sessilibus paucifloris.

Semococh, Depart. Alta Verapaz, Guatemala, alt. 600–900^{m}, Apr. 1905 (*Robert Hay*).

Rondeletia Thiemei Donn. Sm. (§ ARACHNOTHRYX Benth. et Hook.)—Pilosa. Folia parva lanceolato-elliptica utrinque, sursum longius acutiusque, curvilineo-attenuata subsessilia supra scabriuscula subtus cinereo-pilosa. Panicula sessilis parva ovalis, axibus racemiformibus vel cymuliferis. Calycis segmentum quartum lanceolatum ceteris subulatis 3-plo longius.

Frutex, ramulis et panicula cinereo-velutinis. Folia 5–8^{cm} longa 2–2.5^{cm} lata supra punctulata, stipulis triangularibus subulato-acuminatis 3–4^{mm} longis. Panicula terminalis 5–6^{cm} longa foliaceo-bracteosa, axibus patentibus, bracteolis linearibus 4–6^{mm} longis, pedicellis 1–3^{mm} longis, floribus tetrameris singulis vel 2–3-nis, cymulis pedicellatis. Calycis pilosi segmentum maximum 5–6^{mm} longum 3-nervium. Corollae tubus pilosus tenuiter cylindricus 8–10^{mm} longus, os nudum exannulatum, lobi subrotundi 3^{mm} longi crenati utrinque glabri. Capsula globosa 5^{mm}-diametralis pilosa lobis calycinis coronata, seminibus numerosis oblongo-cubicis scrobiculosis.

Río Chamelecón, Depart, Santa Bárbara, Honduras, alt. 400^{m}, Jan. 1888, *C. Thieme*, n. 5276 ex Pl. Guat. &c. quas ed. Donn. Sm.

BIDENS COREOPSIDIS DC., var. **procumbens** Donn. Sm.—Plerumque 5-foliolata, foliolis tenuiter lanceolatis subglabris, corymborum axibus filiformibus, acheniis margine dense barbatis, aristis parce hispidulis.

Prope Secanquim, Depart. Alta Verapaz, Guatemala, alt. 550^{m}, Jan. 1905, *Maxon et Hay* (n. 3162).

Hectia dichroantha Donn. Sm.—Paniculae rami abbreviati simplices continue denseque racemoso-floriferi, racemis cylindricis, floribus singulis. Perianthii segmenta acuta subaequalia pedicello bis breviore adjecto bracteolam paulo superantia.

Folia 3.5–4^{dm} longa perlonge attenuata supra glabra subtus niveo-lepidota spinis corneis inter se 5–10^{mm} distantibus 1–3^{mm} longis crenulata. Scapus cum panicula glaber in sicco purpurascens, vaginis supra oinochrois subtus niveis e basi ovato-lanceolata longissime filiformeque attenuatis 7–9^{cm} longis internodia superantibus. Panicula 5–6^{dm} longa, racemis raro binis sueto inter se 3–7^{cm} distantibus 4–8^{cm} longis, bracteis 1.5–2^{cm} longis uti bracteolae 7–8^{mm} longae lineari-lanceolatis, pedicellis 3^{mm} longis, floribus glabris. Perianthii segmenta discreta ovato-lanceolata, exteriora 5^{mm} longa cum bracteis bracteolisque oinochroa, interiora 6^{mm} longa alba. Florum masculinorum solum cognitorum stamina perianthium aequantia, ovarii rudimentum glabrum.

In collibus declivibus ad flumen *Quililá* prope Santa Rosa, Depart. Baja Verapaz, Guatemala, alt. 1600^{m}, Maj. 1905, *O. F. Cook.*

BALTIMORE, MD.

A BACTERIAL DISEASE OF OLEANDER.

BACILLUS OLEAE (Arcang.) Trev.

CLAYTON O. SMITH.

(WITH FOUR FIGURES)

DURING the autumn of 1905 some diseased oleanders were sent from a nursery to the plant pathological laboratory of the University of California. This disease has been occasionally reported as occurring on young oleanders in this state. The trouble affects the stem and leaves (*figs. 1, 2*), forming large, hard, woody knots. These knots were examined by Professor R. E. SMITH and found to contain

FIG. 1.—Oleander, showing knots on stem and leaf from natural infection.

numerous bacteria which were produced in small colonies in the tissue. The general nature of the knot and the close botanical relationship of the oleander and olive immediately suggested to him that the trouble might be caused by the same organism that produces the so-called knot or tuberculosis of the olive. The subject was assigned to the writer for further investigation. The work for the most part was done at the bacteriological laboratory of the University, and thanks are due to C. M. Haring and Professor A. R. Ward, of that laboratory, for their courtesy and suggestions during the investigation.

Fig. 2.—Leaves of oleander, showing knots from natural infection.

The olive knot is a disease of the branches and leaves of the olive tree. It occurs in Egypt, in the olive-growing sections of Europe bordering on the Mediterranean, and is also found in California where the olive is grown. The disease has been known for many years and is even described by Roman writers; but its bacterial origin has only been recognized since 1886, when the organism was discovered by Arcangeli (**1**) and Savastano (**2**). It is found in the knots in what may be called colonies. These appear as clearer or more transparent spots in the callus-like tissue. These growths have their origin near the cambium layer and at length become darker in color. About this colony hypertrophy of the tissue takes place, as a natural effort of the plant to heal the injury caused by the bacteria. This same process of healing would take place in mechanical injuries. The result is that much soft, spongy tissue is formed that makes a rather favorable place for new bacterial growth, which means a new formation of callus tissue and hence an increase in the size of the knot.

These large knot-like growths of the olive may be found on the leaves, branches, and trunks, few in number or in great abundance. They must not be confused with those caused by insects, and they are also distinct from the enlargements formed on the roots of the Leguminosae by bacteria. Badly diseased trees show scant foliage, limited growth, and occasional dead branches.

The cultural characteristics of the olive knot organism have been studied by SAVASTANO (**5**) and seem to agree quite well with those observed during this study. The following is a portion of the translation of SAVASTANO'S account of the disease as published by PIERCE (**7**):

> This microorganism is a bacillus of medium size; length three to four times its width; it is isolated, but is sometimes joined into chains; the extremities are slightly rounded off. In drops of bouillon it has a distinct movement. The colony has a variable form, from round to oval, with a well-defined margin. In the beginning it is uniformly pointed; later it forms one or two peripheral circles. It is whitish by reflected light, cedar color by transmitted light. The bacillus lives well in ordinary culture media (bouillon, potato, gelatin, agar). The culture has a relatively long life; cultures made in March were still living in June. In short, degeneration begins in about three months. On potato it lives very well and develops rapidly; the colonies are at first like so many round dots, translucent straw color, which, as they develop, form on the surface of the potato a uniform stratum, translucent, and of a deeper color. The bacillus acquires greater dimensions. On gelatin plates it lives very well, with characters and forms as above indicated. In the tubes of gelatin (*a becco*) the culture presents the appearance of a uniform stratum, whitish, the margin finely bilobed, reminding one of the margin of a leaf, the whole culture taking the form of a spatulate leaf. It is slightly dichroic. In tubes of agar (*a becco*) the culture is identical with the preceding, the margin is less bilobed. The culture by needle in gelatin presents a uniform, transparent, finely pointed appearance. On the surface of the meniscus the form is irregularly rounded, with a finely lobed margin, as in the preceding.

In the study of the present disease, the organism was first isolated from the oleander in the manner described below. Inoculations were then made on the oleander and olive. Positive results were obtained in all cases. No effort was made to try inoculations on other plants. SAVASTANO (**5**), however, failed to make successful inoculation with the olive knot organisms on peach, plum, apricot,

FIG. 3.—Knots on olive caused by artificial infection from pure culture: *a*, on leaves; *b*, on tree inoculated in the open. *c*, large knot and smaller knots on plants growing under glass.

grape, fig, pear, apple, bitter orange, lemon, rose, *Abies excelsa*, *A. pectinata*, and *Cedrus Libani*. He did not experiment with the oleander, however, or any other plant related to the olive.

It required considerable time in the writer's experiments for the disease to develop, though in a month's time the first indication of tissue enlargement could be observed. This continued to increase until on the olive quite a knot was formed in two month's time (*fig. 3*). Often the infection did not produce such a large knot as indicated in *fig. 3*, but smaller swellings of the tissue. In this inoculation work agar cultures, 48 hours old, were used, except on one occasion when a bouillon culture was tried. Either gave equally satisfactory results. The visible effects of the inoculations showed sooner on the oleander, but their size and the rapidity of knot-formation seems to depend upon the rapidity with which the plant is growing, as has been before observed by SAVASTANO (**4**) in his study of the olive knot. The organism grows on both the stem and the leaves. In one experiment a leaf of an oleander near the top of the plant was inoculated on the midvein; this inoculation grew well, and from it secondary natural infections resulted on the stem. It was not difficult to trace the new infections on the stem to the very base of the petiole of the diseased leaf. Infection (*fig. 4*) took place probably through the stomata and lenticels. Checks were used by making punctures with a sterile needle, but these gave no knot formations.

The lesions and growth on the hosts were quite different. On the oleander at first there was a slight enlargement of the tissue that became somewhat rounded at the point of infection. After a time, as the new growth continued, there was a splitting of the epidermis in a longitudinal direction, forming a cleft (*fig. 4*). After this a spongy growth formed, which is rather dark in color and contains numerous small colonies of the bacteria. On the olive there was the same enlargement of the tissue as in the oleander, but the formation of the new growth was much more rapid, regular knots being soon formed by the growing out of the new tissue. This took place in the olive rapidly, while in the oleander it was only in the advanced stages that this new callus tissue grew into a knot-like formation. The knots on the olive agreed in appearance with specimens of the typical knots as it occurs in California, and with the illustration as given by PIERCE (**7**), BIOLETTI (**8**), and ERWIN SMITH (**9**).

The original cultures were made from the diseased tissue of the oleander by first cutting away the outside tissue with a scapel, steri-

FIG. 4.—Knots on oleander leaves and stem caused by artificial infection from pure culture.

lized by flaming. When this was done, the small colonies could be seen in the tissue as dark clear places; these were touched with a sterile platinum needle, and a tube of ordinary meat bouillon was inoculated. Several such tubes were inoculated from the knots, and in about two or three days there was abundant growth. From these tubes dilution cultures were made on agar in Petri dishes. Other dilution cultures in Petri dishes were then made from ten of the bouillon tubes, and the uniformity with which one form of colony appeared in the Petri plates seemed to indicate quite conclusively that this was the organism causing the disease. Transfers were then made from these colonies to agar tubes and thence to various culture media.

CULTURAL CHARACTERISTICS.—The organism was grown on the ordinary culture titrated to $+1.5$ to phenolphthalin and grown at room temperature.

Morphology.—The organism is a motile rod with rounded ends, $1.5–2.5 \times 0.5–0.6\ \mu$. It is usually solitary, but may occur in pairs. Organism direct from the plant as well as from the pure culture shows motility. The size as above given was from a preparation made directly from the tissue.

Agar slant.—On agar growth appeared in about twenty-four hours, as a very thin, grayish-white surface growth. This spread quite rapidly over the surface, especially near the lower portion of the tube. Sometimes small roundish colonies appeared at the side of the growth along the stroke. In cultures a week old the growth is white by transmitted and reflected light. The growth is very thin and scarcely perceptible at first. The condensation water becomes clouded and white.

Agar plate colonies.—On agar plates the colonies become visible after three days. The deeper ones are small, globose, or biconvex with sharp entire margins. The surface colonies are larger and more spreading, circular in outline, whitish in color, and somewhat more dense in center than at margin. The deeper ones often have a straw or cedar color as observed by SAVASTANO. The surface colonies measure $2–4^{mm}$ in diameter when four days old. They are more vigorous than colonies in gelatin of the same age.

Glycerin agar.—Growth much the same as in agar, except more vigorous, and hence a thicker surface growth resulted. Numerous small colonies also developed on surface.

Gelatin stab.—Growth takes place along the stab and also on the surface of the media. The growth along the puncture was filiform; on the surface it was thin, spreading from the point of puncture, the margin undulatory to lobate-lobular. No liquefaction.

Gelatin plate colonies.—These appeared in two to three days. The deep colonies much the same as those in agar Petri plates. Surface colonies more spreading, forming a very thin growth with irregular undulatory margins, some darker in color than surface colonies. Surface colonies under low power showed the center to be denser than the margin and finely reticulated. Toward the margin the reticulations are much coarser than in the center.

Potato.—Growth was vigorous and characterized by always being straw color. The growth was quite markedly raised above the surface and soon covered the entire plug.

Bouillon.—In meat bouillon growth appeared after two days as a fine granular substance that remained in suspension. The culture is at first slightly acid to litmus, but becomes alkaline after two weeks.

Glucose bouillon.—Growth the same as in the meat boullion, with the same reactions. The change from acid to alkaline reaction is much slower than in the other media.

Saccharose bouillon.—Growth at first more vigorous than in either the bouillon or glucose bouillon; acid at first, neutral after seven days, and alkaline in two weeks.

Lactose bouillon.—Showed the same general characteristics as saccharose, acid at first, then neutral and alkaline after two weeks.

Litmus milk.—Showed no change until ten days, when there was a distinct alkaline reaction. No coagulation ever occurred. After fifteen days the medium was quite blue, with a slight whitish precipitate at the bottom of the tube. This was not granular, but subgelatinous, and when shaken into solution settled again to the bottom. In a tube two months old the liquid becomes very blue and alkaline.

Milk.—Showed no change except a slight yellowing in color.

Scarcely any experimental work was done in growing the Bacillus at different temperatures. SAVASTANO (**4**) states the optimum temperature for the olive knot to be between 32–38° C, and SMITH (**9**) has still further restricted the limits of best growth to between 35–37.8° C. Several experiments were conducted by the writer with the oleander organism in temperature about 35.5° C, and no growth took place on agar, bouillon, or potato after four days, although there was good growth in the inoculated bouillon tube at room temperature.

All the liquid media become at first acid to litmus, but change to an alkaline reaction in about two weeks. The media used were all titrated to +1.5 to phenolphthalein. This would be slightly alkaline to litmus, so the growth of the organism caused first an acid, then an alkaline reaction. All the cultural characteristics of the oleander organism, so far as possible, were compared with those described from the olive organism. There seems to be a very close agreement, and without question the organism is identical.

From knots produced by artificial inoculations on olive and oleander the organism was isolated (in the same manner as described before) and grown in the same media as was the original culture from the oleander. These two series agreed perfectly in culture characteristics with one another and with the original culture.

The organism also was isolated from naturally infected olive knots in the same manner as for the oleander. Growth on various culture media showed biochemical and cultural characteristics that agreed with those observed by the writer for the oleander knot; and with those described by SAVASTANO in his study of the olive knot.

This oleander disease is not believed to be a new trouble, but similar to the one found on olives. They are both caused by a motile rod (Bacillus) that grows well on the ordinary culture media, and will cause infection of the olive and the oleander. This infection at length causes characteristic lesions and knot-like growths on the stem and leaves. The knots produced on the olive by the oleander organism agree with typical knots as found on cultivated olives in California, and with various illustrations of the olive knot. The cultural characteristics of the two are similar in all essential respects.

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LITERATURE CITED.

1. ARCANGELI, G., Sopra la malattie dell' olivo detta volgarmente rogna. Pisa. 1886.
2. SAVASTANO, L., Les maladies de l'olivier et la tuberculose en particulier. Compt. Rend. **103**: 1144. 1886.
3. ——, Les maladies de l'olivier; hyperplasies et tumeurs. *Idem* 1278. 1886.
4. ——, Tuberculosi, perplasie e tumori dell' olivo. I e II Memoria. Naples. 1887.
5. ——, Il baccillo della tuberculosi dell' olivo, nota suppletiva. Rend. Lincei **5**: 92–94. 1889.
6. PRILLIEUX, E., Les tumeurs à bacilles de l'olivier, etc. Compt. Rend. **108**: 249. 1891.
7. PIERCE, NEWTON B., Tuberculosis of the olive. Jour. Mycol. **6**: 148–153. 1891.
8. BIOLETTI, F. T., The olive knot. Calif. Agric. Exp. Sta. Bull. 120. 1898.
9. SMITH, ERWIN F., Bacteria in relation to plant diseases. **1**: 10. 1905.

CURRENT LITERATURE.

BOOK REVIEWS.

Another botanical dictionary.

THIS Italian book is in a measure both a dictionary, with its mere definition of terms, and an encyclopedia, with its more elaborate treatment of topics and brief biographies of celebrated botanists.[1] In its plan, therefore, it departs widely from JACKSON'S *Glossary;* and it departs from it still more widely in mechanical execution. For it is published by ULRICO HOEPLI of Milan whose series of dictionaries and manuals is famous. It is 11×16^{cm}, printed on thin flexible paper, with narrow margins and small but clear type, bound in half vellum, and though it contains nearly a thousand pages it is less than 4^{cm} thick. Every detail is appropriate to its use and the book is therefore a model of convenience.

In substance the work is unexpectedly good. The definitions of the simpler terms are usually clear and succinct, and the treatment of topics is full enough and is accompanied by citation of enough of the important literature to make the book of real value for reference. A few figures will indicate the extent of some topics. Thus to *nutrizione* are devoted nearly 36 pages; to *tessuti*, 10 pages; to *simmetria*, 6 pages; to *variazione*, 7 pages; to *germogliamento*, 6 pages; to *classificazione*, 8 pages; and so on. On the whole the assignment of space is made with good judgment.

The only adverse criticism that need be made is that the author has apparently not always assimilated fully the modern morphology that he is endeavoring to state. In consequence seeming contradictions and limitations occasionally appear. Thus the *sporofito* seems to belong only to ferns and spermatophytes; while the *sporogonio* appertains to the bryophytes. *Sporangio* is defined and discussed only with reference to pteridophytes, and *spore* would seem to be restricted to "cryptogams." Yet in other topics the relations of the microspores of spermatophytes are recognized and properly described, while the alternation of generations and heterospory are concisely but clearly treated.

On the whole there are probably as few shortcomings as could be expected and as many excellences as could be attained by any one who undertakes such a task. Cooperation, however, is fast coming to be necessary in work of such a scope.—C. R. B.

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[1] BILANCIONI, EUG., Dizionario di botanica generale. Milano: Ulrico Hoepli. 16mo. pp. xx+926. *L* 10.

MINOR NOTICES.

Botanical papers at the St. Louis Congress.—Volume V[2] of the series being published by the Congress of Arts and Science held in connection with the St. Louis Exposition contains the botanical papers. The department of biology was divided into eleven sections, and twenty-five principal papers were read. Those of special interest to botanists, in the order of their appearance in the volume, are as follows: Development of morphological conceptions, JOHN M. COULTER; The recent development of biology, JACQUES LOEB; A comparison between artificial and natural selection, HUGO DEVRIES; The problem of the origin of species, C. O. WHITMAN; Plant morphology, F. O. BOWER; The fundamental problems of present-day plant morphology, K. GOEBEL; The development of plant physiology under the influence of the other sciences, J. WIESNER; Plant physiology, present problems, B. M. DUGGAR; The history and scope of plant pathology, J. C. ARTHUR; Vegetable pathology an economic science, M. B. WAITE; The position of ecology in modern science, O. DRUDE; The problems of ecology, B. L. ROBERTSON; Relations of bacteriology to other sciences, E. O. JORDAN; Some problems in the life history of pathogenic microorganisms, THEOBALD SMITH.

All of these papers have been published in various journals, notably in *Science*, but it is convenient to know that they are all accessible in a single volume.—J. M. C.

Index Filicum.—The eleventh fascicle of CHRISTENSEN's work has just appeared,[3] carrying the references from *Trichomanes Giesenhagenii* to the end of the list. There follow a list of additions, a list of corrections, and the beginning of a catalogue of literature arranged alphabetically.—J. M. C.

Trees of Java.—KOORDERS and VALETON[4] have published another fascicle of additions to the known arboreal flora of Java, containing the Moraceae. Seven genera are represented, including 95 species, 83 of which belong to Ficus, under which two new species are described.—J. M. C.

Cyperaceae.—The second part of HUSNOT's synopsis of the Cyperaceae of France, Switzerland, and Belgium has appeared,[5] completing the list of species, and closing with a full index.—J. M. C.

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[2] Congress of Arts and Science, Universal Exposition, St. Louis, 1904. Edited by HOWARD J. ROGERS. Volume V. Biology, Anthropology, Psychology, Sociology. pp. xi+882. Boston and New York: Houghton, Mifflin and Company. 1906.

[3] CHRISTENSEN, C., Index Filicum, etc. Fasc., 11. Copenhagen. H. Hagerup. 1906. 3*s.* 6*d.*

[4] KOORDERS, S. H., and VALETON, TH., Boomsoorten op Java. Bijdrage no. 11. Mededeel. Depart. Landb. no. 2. pp. 277. Batavia, 1906.

[5] HUSNOT, T., Cypéracées: descriptions et figures des Cypéracées de France, Suisse et Belgique. Part II. pp. 49–83. *pls. 13–24.* Cahan, par Athis (Orne): the author. 1906. 5*fr.*

NOTES FOR STUDENTS.

Mosaic disease of tobacco.—In an extensive account of the mosaic disease of tobacco, which he has been investigating for a number of years, HUNGER[6] deals somewhat radically with the theories that have been advanced to account for the disease, and gives, as he believes, a new explanation. The earlier bacterial theories of MAYER, PRILLIEUX, DELACROIX, and others are treated only as matters of historical interest, since they are based on insufficient evidence. The more recent work of IWANOWSKI receives a more extended notice, although his view of the bacterial nature of the disease is likewise refuted, as HUNGER has been unable in his own investigations to corroborate IWANOWSKI's work. BEIJERINCK's theory that the disease is caused by an active fluid substance, itself capable of growth, is discredited on the ground that BEIJERINCK was unable to show that the virus was able to increase in quantity outside of the plant, and that his proof of the fluid nature of the virus (diffusion in agar) is not sufficient. Against the enzyme theory of WOODS the author raises two principal objections: (1) the transferability of the disease without limit does not accord with the properties of enzymes, whose activity is diminished by extreme dilution; (2) the virus of the mosaic disease has the property of being able to diffuse through parchment, a property not possessed by enzymes.

HUNGER advances the view that the mosaic disease is due exclusively to disturbances of metabolism, the outward manifestation of which is the peculiar form of variegation seen in the leaves. That the mosaic disease, to whatever cause it may be attributed, is a result of disturbances of the metabolic processes of the plant is beyond cavil; how this statement brings us any nearer to an explanation of the ultimate cause of the disease is beyond our comprehension. The author regards the disease as a sort of latent property possessed by tobacco plants, in which it may develop spontaneously if conditions are favorable, or to which it may be communicated by grafting and other methods. It is to be regarded as a kind of communicable variability! The active cause of the disease he regards as a toxin normally produced in the plant, but not injurious except under special conditions, when it accumulates in excess of the normal amount. The toxin is not like BEIJERINCK's substance, capable of active growth, but is capable, when entering into a normal cell, of producing there catalytic effects, in consequence of which the toxin is there regenerated secondarily. In the words of the author, it is physiologically autocatalytic, all of which is perhaps merely a more extended theoretical explanation of what is ordinarily termed growth. HUNGER discusses also the etiology of the disease, and the probable relation of the methods of selection of tobacco practised at Deli to the rapid increase of the disease in the Sumatra tobacco districts. He points out that in order to obtain a high grade wrapper-leaf it has for generations been the practice of the tobacco growers to select for seed the plants with the thinnest leaves. This

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[6] HUNGER, F. W. T., Untersuchungen und Betrachtungen über die Mosaik-Krankheit der Tabakspflanze. Zeitschr. Pflanzenkr. **15**:257–311. 1905.

selection has resulted in a race of plants degenerate from the standpoint of their power to resist unfavorable conditions. In the fields, even under usual conditions, a large percentage of the plants wilt on hot days. The reduction of thickness of the leaf is held in large measure responsible for the occurrence of the mosaic disease. A lesser though important influence is also attributed to the direct action of the soils.—H. HASSELBRING.

Microsporangia of Pteridosperms.—In 1905 KIDSTON published a preliminary note on the occurrence of microsporangia in connection with the foliage of Lyginodendron.[7] He has now published the full paper,[8] with detailed discussion and illustration. He first elaborates the evidence that *Sphenopteris Höninghausi* Brongn. and *Lyginodendron Oldhamium* Williamson are identical plants, and of course *Crossotheca Höninghausi* is the fertile pinnule of the former. It follows that the sporangia found on this species of Crossotheca are the microsporangia of *Lyginodendron Oldhamium*, a well-known pteridosperm. This rules out Miss BENSON'S claim that *Telangium Scotti* represents the microsporangia of this Lyginodendron.

The microsporangia are borne on modified pinnae, associated with sterile pinnae. The fertile pinna is oval, entire, on a short thick pedicel, and on the under side of the blade six to eight fusiform bilocular sporangia are borne, which bend inward at an early stage so that their pointed apices meet, forming a sort of hemispherical sorus. Later they spread apart and appear as a fringe hanging from the margin of the pinnule. In all cases the microspores are present, but no internal structure seems to be evident. The genus Crossotheca contains eight species, a new one being described in this paper, and perhaps it is safe to assume that all of them belong to the pteridosperms.

In a general discussion of the occurrence of fern-like plants, KIDSTON comes to the conclusion that the pteridosperms (including all Cycadofilices) are undoubtedly the oldest group of fern-like plants of which we have evidence, being plainly represented in the upper Devonian; that in the Lower Carboniferous pteridosperms were still dominant, true ferns being feebly represented, if at all, by the Botryopterideae; that in the Upper Carboniferous the same relative representation continued. It seems highly improbable, therefore, that the pteridosperms could have descended from true ferns, and KIDSTON is inclined to believe that there is no more relationship between the two groups than that of a common ancestry for pteridosperms and eusporangiate ferns. In summing up his conception of the most probable lines of descent of the existing ferns and cycads, he indicates three lines: an independent one, leading from Botryopterideae (of unknown origin) to the leptosporangiate ferns, and two lines converging in common but unknown ancestral forms, one leading to the Marattiaceae, the other through pteridosperms to the cycads.—J. M. C.

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[7] BOT. GAZETTE **41**:219. 1906.

[8] KIDSTON, ROBERT, On the microsporangia of the Pteridospermae, with remarks on their relationships to existing groups. Phil. Trans. Roy. Soc. London B. **198**:413–445. *pls. 25–28.* 1906.

Experiments with Hieracium.—OSTENFELD and ROSENBERG have undertaken a series of experimental and cytological studies of the species of Hieracium. ROSENBERG has published[9] a preliminary report of some of his results; but the first paper of the series has just been received. It is by OSTENFELD,[10] reporting the results of castration and hybridization experiments. The castration experiments, carried on in 1903, 1904, and 1905, resulted in showing that in the genus Hieracium there are apogamous species, non-apogamous species, and transition species, and that the three subgenera conform in a general way to this division; Stenotheca having typical fertilization (the most primitive stage); Pilosella being intermediate, with both apogamous and non-apogamous species (the former in the majority); and Archieracium being entirely apogamous (except the *H. umbellatum* group). Attention is called to the fact that Taraxacum has "gone a little farther," all its species being apogamous.

The hybridization experiments are only in their inception, but the following results may be noted: a hybrid was produced between *H. pilosella* and *H. aurantiacum*, with greatly reduced fruiting power; *H. excellens*, itself probably a natural hybrid and producing only abortive pollen, gave hybrids by crossing with *H. aurantiacum* and *H. pilosella;* the hybrids arising from the same cross are heterogeneous; the fruiting power of hybrids is very slight.—J. M. C.

Infection experiments with mildews.—REED[11] has added a further contribution to the work inaugurated by NEGER and extended by MARCHAL and SALMON, bearing on the transferability of physiological forms of the Erysipheae from one specific host to another within a closely related group of plants. The results in general confirm the conclusions of previous investigators; namely, that there exist races of *E. graminis* and other species of mildews which have become specifically adapted to a single species, or more rarely to several species of one genus of host plants. REED finds, for example, that E. *graminis* from *Poa pratensis* will not infect other species of Poa except in some instances. Thus *P. nemoralis* is sometimes infected, while *P. trivialis* and *P. compressa* are infected very rarely. By this and other investigations the fact that a high degree of specialization exists in the Erysipheae, as in other groups of fungi, has been definitely established. While further demonstration of the existence of biological races is of less importance, the facts ascertained in this field of research furnish an excellent basis for other investigations, as for instance, the question of the permanency of these races, the problems connected with abnormal predisposition of the host plants, and others, some of which have already received attention. —H. HASSELBRING.

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[9] Ber. Deutsch. Bot. Gesells. **24**: 1906.

[10] OSTENFELD, C. H., Experimental and cytological studies in the Hieracia. I. Castration and hybridization expermients with some species of Hieracia. Bot. Tidssk. **27**: 225–248. *pl. 1.* 1906.

[11] REED, GEORGE M., Infection experiments with *Erysiphe graminis* DC. Trans. Wis. Acad. Sci. **15**: 135–162. 1905.

Turgor in yeast.—PANTANELLI having examined the regulation of turgor in certain fungi and distinguished "cell pressure" into two factors, (1) osmotic pressure or turgor, due to solutes, and (2) tension, due to imbibition, has investigated by the same methods the turgor regulation in yeast derived from Roman bread.[12] He finds that during fermentation turgor at first increases, then remains constant, and finally diminishes when the nutritive value of the medium becomes much lowered. The power of osmotic regulation depends primarily upon nutrition. If the foods are temporarily removed without altering the concentration of the medium, the turgor and the tension diminish rapidly, the plant being compelled to use its own reserves, forming vacuoles. If grown in water or allowed to dry slightly, turgor diminishes, but the tension increases, in the first condition until death, in the second up to a maximum, after which it diminishes greatly before death. With age the power of osmotic regulation is gradually lost. Aeration facilitates it so much that it seems admissible to say that the Roman yeast lives during and after fermentation only because it falls into a state of narcosis more or less profound.—C. R. B.

Blast of rice.—METCALF[13] has recently published an account of the "blast" of rice with short notes on other rice diseases. This blast is characterized by lesions at one or more of the nodes of the stem above which the stem dies. It has often been confused with other diseases or injuries and the true extent of its damage not realized. The disease is promoted by resting the land or by applying nitrogenous fertilizers. It can be produced in healthy plants by inoculations directly from diseased plants, but the organism causing the disease has not yet been fully determined. The use of lime and marl with potash and phosphorus is recommended as fertilizer treatment that tends to reduce the tendency to blast. The disease is prevented by spraying with Bordeaux mixture, but this treatment is not practicable with this crop. The search for immune plants has been of no avail up to this time.—E. MEAD WILCOX.

A new chestnut disease.—MURRILL[14] has described a new and serious disease of the native chestnut, which is epidemic in many parts of New York City and threatens to destroy all the chestnut trees of that region. The disease is also known to occur in New Jersey, Maryland, District of Columbia, and Virginia. "The fungus attacks twigs, branches, and trunks, irrespective of size or position, and usually proceeds in a circle about the affected portion until it is completely girdled." It is described as a new species of Diaporthe (*D. parasitica*). —J. M. C.

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[12] PANTANELLI, E., Richerche sul turgore delle cellule di lievito. Annali di Botanica **4**:1–47. 1906.

[13] METCALF, H., A preliminary report on the blast of rice, with notes on other rice diseases. Bull. N. Car. Exp. Sta. 121:1–43. 1906.

[14] MURRILL, W. A., A new chestnut disease. Torreya **6**:186–189. 1906.

Haustorium of Santalum.—BARBER[15] has begun the publication of a series of papers on root parasitism, the first one dealing with *Santalum album*, giving an account of the early stages of the haustorium as far as penetration into the host's tissues. This is a somewhat fuller account than that published by the author in the *Indian Forester* and noticed in this journal.[16] A second paper is promised which will describe the structure of the mature haustorium. Investigation of the mutual influence of host and parasite is also in progress.—J. M. C.

A new red clover.—BRAND[17] has published the results of a study of a red clover not hitherto used in the United States as a forage plant. The seed is from Orel, in the "Black Earth" region of Russia, and the plant possesses advantageous qualities that make its introduction desirable. Perhaps its most striking mark in the field is the almost complete lack of hairiness; but it is the general leafiness and the persistence and number of basal leaves that suggest for the new variety the name *T. pratense foliosum* Brand.—J. M. C.

Plant diseases in Nebraska.—HEALD[18] has published notes on the distribution and severity of numerous diseases of cultivated plants in Nebraska during 1905, together with suggestions as to treatment of the various troubles. This in a way constitutes a handbook of plant diseases in Nebraska. He has also published an account of a rot of apples due to *Sclerotinia fructigena*,[19] and a disease of the cottonwood due to *Elfvingia megaloma*,[20] once a member of the genus Polyporus.—E. MEAD WILCOX.

Pteridophytes of southern Florida.—EATON[21] has put on record his observations on the pteridophytes of southern Florida during three excursions. The purpose is to bring together the little-known species, with careful descriptions, so that they may be more readily recognized by students of the flora. The paper is also a contribution to geographical distribution. Most of the plants described are ferns, among which is a new species of Tectaria.—J. M. C.

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[15] BARBER, C. A., Studies in root parasitism. The haustorium of *Santalum album*. 1. Early stages, up to penetration. Memoirs Depart. Agric. India **1**: no. 1. pp. 30. *pls. 7.* 1906.

[16] BOT. GAZETTE **40**: 159. 1905.

[17] BRAND, CHARLES J., A new type of red clover. U. S. Dept Agric., Bureau Pl. Ind., Bull. 95. pp. 45. *pls. 3.* 1906.

[18] HEALD, F. D., Report on the plant diseases prevalent in Nebraska during the season of 1905. Rep. Neb. Exp. Sta. **19**: 19–81. 1906.

[19] HEALD, F. D., The black rot of apples due to *Sclerotinia fructigena*. Rep. Neb. Exp. Sta. **19**: 82–91. *pls. 1–2.* 1906.

[20] HEALD, F. D., A disease of the cottonwood due to *Elfvingia megaloma*. Rep. Neb. Exp. Sta. **19**: 92–100. *pls. 1–4.* 1906.

[21] EATON, A. A., Pteridophytes observed during three excursions into southern Florida. Bull. Torr. Bot. Club **33**: 455–486. 1906.

Pollen tube of Houstonia.—MATHEWSON[22] has studied the advance of the pollen tube in Houstonia, coming to the conclusion that any mutual influence between the tube and the cells with which it comes in contact is very slight; and that the direction of the advance of the tube seems to be chiefly in response to a stimulus originating in the egg apparatus, perhaps in the egg itself.—J. M. C.

Operculina.—HOUSE[23] has published a synopsis of the genus Operculina as the second paper of his series on North American Convolvulaceae. It comprises about twenty tropical species, which are perhaps better known to many botanists under Convolvulus and Ipomoea. In North America fifteen species are recognized, two of them being described as new.—J. M. C.

Influence of temperature upon flowering of fruit trees.—Ecologists and physiologists will be interested in the phenological notes presented by SANDSTEN[24] relative to the influence of temperature and other factors upon the time of flowering of certain fruit trees. He reaches the conclusion that "physiological constants can be formulated from the climatic conditions during the ten months preceding the time of flowering."—E. MEAD WILCOX.

Effect of light on growth.—SELBY[25] has extended the work of MACDOUGAL to include four other species, mostly those which are latex-bearing. MACDOUGAL'S conclusions that light does not have a retarding influence on growth and that it does stimulate morphogenic processes in the meristematic tissues are confirmed.—RAYMOND H. POND.

Varieties of roots developed by English ivy.—Miss RANDOLPH[26] finds that *Hedera Helix* may be induced to form in all seven kinds of roots according to the conditions of moisture.—RAYMOND H. POND.

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[22] MATHEWSON, C. A., The behavior of the pollen tube in *Houstonia coerulea*. Bull. Torr. Bot. Club **33**:487–493. *figs. 3.* 1906.

[23] HOUSE, H. D., Studies in the N. Am. Convolvulaceae. II. The genus Operculina. Bull. Torr. Bot. Club **33**: 495–503. 1906.

[24] SANDSTEN, E. P., Conditions which affect the time of the annual flowering of fruit trees. Bull. Wisc. Exp. Sta. 137: 1–21. 1906.

[25] SELBY, A. D., Studies in etiolation. Bull. Torr. Bot. Club **34**:67–75. *pls. 2. figs. 4.* 1906.

[26] RANDOLPH, HARRIET, The influence of moisture upon the formation of roots by cuttings of ivy. Bull. Torr. Bot. Club **34**:93–99. *figs. 4.* 1906.

NEWS.

DR. IRA D. CARDIFF, Columbia University, has been appointed professor of botany in the University of Utah, Salt Lake City.

DR. MAX KÖRNICKE, University of Bonn, has received the Buitenzorg grant of the German government for 1906-7 and left for this station August 29.

DR. C. A. J. A. OUDEMANS, the mycologist, emeritus professor of botany in the University of Amsterdam, died recently at Arnhem at the age of eighty years.

DR. D. H. CAMPBELL, Stanford University, has returned after an absence of a year, some of which was spent in South Africa and the Botanical Gardens at Peradeniya and Buitenzorg.

MR. LEROY ABRAMS, of the Smithsonian Institution, formerly instructor in botany in Leland Stanford University, has been appointed assistant professor of systematic botany in the University.

DR. BRADLEY M. DAVIS will spend next winter in Cambridge, Mass. His immediate work will be the completion with MR. BERGEN of a laboratory and field manual to accompany the *Principles of Botany* which has recently appeared from the press of Ginn & Company.

THE GRANTS made for scientific research at the York meeting of the British Association include the following botanical grants: Physiology of heredity, £30; South African cycads, £35; Botanical photographs, £5; Structure of fossil plants, £5; Peat moss deposits, £7; Marsh vegetation, £15.

THE AUTUMN COURSE of public lectures announced by the Field Museum of Natural History, Chicago, contains two botanical titles as follows: October 20, "The century plants, and some other plants of the dry country," by Dr. WILLIAM TRELEASE; November 17, "Some phases of plant distribution," by Dr. J. M. GREENMAN.

COUNT OSWALD DE KERCHOVE DE DENTERGHEM, who upon the sudden death of Professor LÉO ERRERA was appointed president of the International Botanical Congress to be held in Brussels in 1910, died on March 20, at the age of sixty-two. He was president of the Royal Society of Agriculture, and of the Botanical Society of Gand, a senator, and ex-governor of Hainault.

AT THE University of Chicago, Dr. W. G. LAND has been promoted to an associateship, and Mr. L. L. BURLINGAME has been appointed assistant in morphology. Dr. FLORENCE LYON resigned at the close of the summer quarter, and shortly thereafter was married to Mr. S. VINCENT NORTON, of Akron, Ohio. The number of students registered for research work in the autumn quarter is the largest in the history of the department.

AT THE CONCLUDING MEETING of the International Conference on Hybridization and Plant Breeding the Veitch gold memorial medals were presented to Mr. W. BATESON, F.R.S., the president of the conference, Professor JOHANNSEN, Professor WITTMACK, and Professor MAURICE DE VILMORIN. Banksian silver-gilt medals were awarded to Miss E. R. SAUNDERS, lecturer on botany at Newnham College, and Mr. R. H. BIFFEN, for eminent services to scientific and practical horticulture.—*Nature.*

THE BOTANICAL SOCIETY OF AMERICA will meet in New York City in Convocation week, beginning December 27, in affiliation with the A. A. A. S. This meeting, the first after the union of the three constituent societies, will be an important one, as questions of future policy are likely to be brought before the society. The sessions will be arranged, in cooperation with the officers of Section G, so as to avoid conflict. Members are requested to send to the Secretary (WILLIAM TRELEASE, Missouri Botanical Garden, St. Louis), at the earliest possible date, titles of papers and information as to time and any special facilities required for their presentation. The total number of members at present is 119.

THE BOTANICAL SUBJECTS for 1907 and 1908 announced for the "Walker Prize," offered annually by the Boston Society of Natural History, are as follows:

For 1907: The structure and affinities of some fossil plant or group of fossil plants. The development of the gametophytes in any little known representative of the Coniferales. The anatomy and development of some order or group of the angiosperms.

For 1908: An experimental study of inheritance in animals or plants. A comparative study of the effects of close-breeding and cross-breeding in animals or plants. A physiological study of one (or several) species of plants with respect to leaf variation. Fertilization and related phenomena in a phenogamous plant. What proportion of a plant's seasonal growth is represented in the winter bud?

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Editors: JOHN M. COULTER and CHARLES R. BARNES

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NOVEMBER 1906

THE OVULE AND FEMALE GAMETOPHYTE OF DIOON.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXXXVI.

CHARLES J. CHAMBERLAIN.

(WITH NINE FIGURES AND PLATES XIII–XV)

ONLY two of the nine genera of cycads have received any considerable attention from morphologists. In these two, Cycas and Zamia, the life history is fairly well known and many of its phases have been studied in great detail. In Stangeria the development of the sporangia has been investigated, and work on the remaining six genera is fragmentary.

Through the courtesy of the Botanical Society of America[1] the writer was enabled to visit the Mexican tropics for the purpose of securing material of Dioon and Ceratozamia. The hearty cooperation of Governor TEODORO A. DEHESA, who is an active educator as well as a statesman, made it possible to collect an abundance of material in a very short time. Mr. ALEXANDER M. GAW, of the State Bureau of Information, Xalapa, Mexico, had many collections of material brought into Xalapa from the field and forwarded to me after my return to Chicago. To both of these gentlemen I wish to express my sincere thanks, since the investigation would have been very limited without their efficient assistance. The photographs used were made by Dr. W. J. G. LAND.

The subject will be treated under the following heads: I. Dioon in the field; II. Material and methods; III. The ovule; IV. The female gametophyte; V. The microsporangium; VI.

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[1] The grant was made in December 1904 by the Botanical Society, at the St. Louis meeting of the A. A. A. S., and was for the purpose of securing material for a morphological study of Dioon and Ceratozamia.

Male gametophyte; VII. Fertilization; VIII. The embryo and seedling. The first four are presented in the present paper; the remaining subjects have been investigated and the results will be published soon.

I. DIOON IN THE FIELD.

Dioon edule occurs in great abundance at Chavarrillo, about 25^{km} east of Xalapa, the capital of the State of Vera Cruz. During March 1904 I made frequent trips through this region and, besides the tedious work of preparing material, was able to make a few observations upon the plant as it occurs in the field. A second trip, devoted largely to field study of both Dioon and Ceratozamia, was made in September 1906. As the results of this trip will be published in a separate paper, only a brief description of the general appearance of Dioon is given at this time.

Associated with Dioon are occasional specimens of a large Opuntia. Orchids and Tillandsias are not infrequent on the trees at the bottom of ravines, though neither of these plants flourish on the rocky slope where Dioon is at its best. In the lower portions of ravines several species of Selaginella are abundant. Dioon is so abundant on the rocky slopes that from a favorable point of view as many as a hundred plants may be counted. Seedlings are numerous and one always meets these and then small crowns before coming upon plants large enough to bear cones. In spite of the seedlings, it is doubtful whether the limited range is being extended.

In habit Dioon resembles *Cycas revoluta* (*fig. 1*). Some call it the "Dolores palm;" but the natives are more likely to call it *Tio Tamal* ("Uncle Tamal"), because they use the large endosperm in making *tamales*. The largest plant measured had a trunk nearly 3^{m} in height, and plants 1–1.5^{m} in height are not infrequent. The trunk often rises obliquely, as shown in the figure, and as noted in taxonomic descriptions.

The age of individuals.—Even in the largest plants the leaf scars are perfectly distinct over the entire surface, so that it is possible to determine with almost absolute accuracy the total number of leaves which a plant has borne. Professor LUIS MURILLO has estimated the age of individual plants by noting the number of leaves in a crown, the duration of the crowns (two years), and the entire number of

FIG. 1.—Ovulate plant of *Dioon edule* on rocky hillside at Chavarrillo, Mexico; the trunk is 1.5^m high.

leaf scars. From such data, the age of one plant with a trunk 1.45^{m} in height and 26^{cm} in diameter was estimated at 970 years. A small plant only 21^{cm} in height is known to have been in cultivation more than 40 years, and was presumably a fine specimen when brought in from the field. In cultivation a crown may persist more than two years, for the crown of a plant in the Washington Park (Chicago) conservatory has remained vigorous for at least five years. It seems probable that MURILLO'S estimate is conservative, and that many of the large plants have reached an age of more than a thousand years.

The trunk.—The trunk is always straight and shows no external evidence of branching; among the thousands of plants observed, one only showing definite branching. The specimen had a Y-shaped trunk, each arm of the Y bearing a large crown. A few specimens were seen with two, three, or four crowns; and one plant had five and another six. The extra crowns do not come from loose buds which might become detached, as is so commonly the case in *Cycas revoluta*, but are all interlocked at the top of the stem. Some of the extra crowns are probably due to injuries received in the removal of cones, while others originate from the germination of seeds which had not fallen to the ground but had remained in the nest of the crown. Buds like those of *Cycas revoluta* also occur; occasionally they are found near the bases of old trunks, and at the top they are quite common. Some of these buds have well-developed crowns and would doubtless grow into independent plants if they should become detached and gain a suitable foothold. Root tubercles were observed but they were infrequent.

The ovulate cones.—In 1904 fruiting plants were not abundant; among plants large enough to bear cones not more than one in ten was in fruit, and among these staminate plants were more numerous than ovulate. In 1906 at least one-third of the larger plants bore cones. I was informed that a plant fruits every other year, and judging from the proportion of plants bearing cones in 1906 this would seem true; but an estimate based upon the proportion of plants bearing cones in 1904 would make the interval very much longer. The ovulate cones are large and ovoid (*figs. 2, 3*). Cones weighing 5^{kg} are common; and one large cone weighed 6^{kg} after

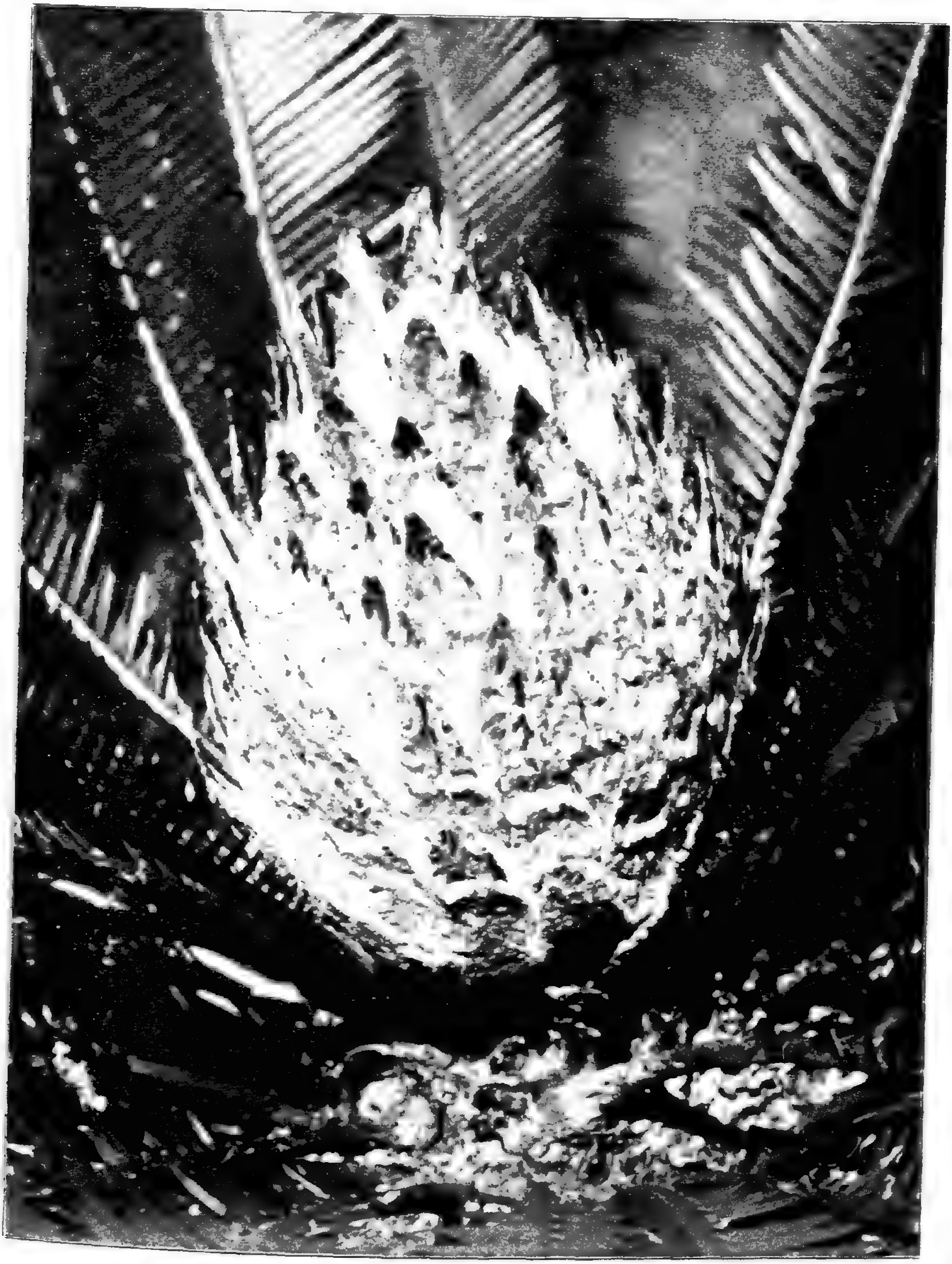


FIG. 2.—Ovulate cone 30^{cm} in length; some leaves have been trimmed away.

it arrived in Chicago, more than two weeks after it had been taken from the plant. This was a March cone and probably would have gained another kilo before June. The length of the mature cone is 20–30$^{\mathrm{cm}}$, and the greatest diameter is 12–20$^{\mathrm{cm}}$. Young cones picked November 1, 1904, five months before the cones reach full size, weighed 1.5–2$^{\mathrm{kg}}$ after reaching Chicago. The single cone rests snugly on the plant at the center of the crown of leaves, the peduncle being entirely concealed, so that it is difficult to remove the cone with a knife. The easiest way is to grasp the cone with both hands and push it firmly to one side until the peduncle snaps with a clean transverse break. After the seeds are ripe the peduncle elongates somewhat, so that the cone often leans to one side, perhaps facilitating the dispersal of seeds. There is a well-developed abscis-

FIG. 3.—Ovulate cone 33$^{\mathrm{cm}}$ in length, showing position of ovules.

sion layer at the base of the petiole of the sporophyll, so that the whole sporophyll drops easily when the seeds are ripe. A second abscission layer, which separates the ovules from the sporophyll, does not mature until a much later period.

II. MATERIAL AND METHODS.

In March the ovulate cone has almost reached its full size, and the staminate cone of the same season has decayed. The first staminate cones were sent from the field on June 30, 1904. These showed the four microspores still held together by the wall of the spore mother cell. From this point to the discharge of the motile sperms a complete series in the development of the male gametophyte was secured. In the female gametophyte the series is complete from the appearance of the archegonium initial to the germination of the seed. The series showing the development of the embryo is very complete.

Nearly all the material was fixed in chrom-acetic acid in various proportions, with or without the addition of osmic acid. The following formula is excellent for the pollen tube structures and for young ovules: chromic acid, 1^{gm}; glacial acetic acid, 4^{cc}; 1 per cent osmic acid, 2^{cc}; water, 100^{cc}. This fluid will not penetrate the microsporangia, and with older ovules it not only causes some plasmolysis but makes the endosperm very hard to cut. After the endosperm has become starchy, better results were secured by using a slight modification of a formula suggested by Dr. LYNDS JONES: 50 per cent. alcohol, 100^{cc}; commercial formalin, 6^{cc}. This reagent penetrates well and fixes rapidly. Iron-alum haematoxylin stains brilliantly after it, but the safranin gentian-violet orange combination does not give as bright a stain as with material fixed in chromic solutions. After this reagent, the starchy endosperm is not so hard to cut. After the stony coat of the ovule has become hard, it is almost impossible to cut it with any knife without injuring the archegonia. For such stages the ovules were sawed in two transversely with a fine wire-like fret saw. The upper part of the endosperm with its archegonia was then trimmed into suitable shape for cutting. The extremely thin blade of the Gillette safety razor, soldered to any suitable handle, is particularly adapted for such trimming, since it causes no damaging pressure as does the wedge-shaped blade of a scalpel or ordinary razor. The nucellus usually remains within the cup-like top of the ovule. Four strokes with a sharp scalpel will cut through the nucellus against the stony background and remove a piece containing the pollen tubes. Methods for studying the living sperms will be given in a second paper. For showing the grosser structures of the ovules, sections 4 or 5^{mm} in thickness were dehydrated and then cleared in xylol. For tracing the vascular bundles, the pseudo-stalks of ovules were cut under water and the bases were placed in eosin. The outer bundles soon become conspicuous on the surface, and the inner bundles are easily traced by removing the endosperm and scraping away the greater part of the inner fleshy layer of the integument.

Most of the sections were stained in safranin and gentian-violet; some were stained in iron-alum haemotoxylin. Magdala red and anilin blue proved to be a good combination, especially for pollen-tube structures, and it is quite convenient, since no clearing agent is necessary, the slides being taken directly from the absolute alcohol and mounted in Venetian turpentine. Overstaining in the Magdala red can be corrected, even after the cover glass is in place, by exposing the slide to direct sunlight for a short time.

III. MEGASPOROPHYLLS AND OVULES.

No other cycad, except Cycas, has such large and leaf-like megasporophylls as Dioon (*figs. 4–6*). Both the leaf-like character of the megasporophylls and their comparatively loose association in the cone are more suggestive of Cycas than of Zamia or Ceratozamia, which are the geographical neighbors of Dioon. The remaining occidental cycad, Microcycas, is too imperfectly described to allow any comparison of the cones.

In Dioon the sporophylls at the base of the ovulate cone are yellowish or greenish, with little hair except along the central portion of the back. There are four or five turns of the spiral of these sporophylls, followed by one or two turns of somewhat hairy sporophylls. The remaining sporophylls are densely covered with long brown hairs, the lower ones on the back and edges and a small portion of the upper part of the inner face, and the rest not only upon the back and edges but upon the entire upper half of the inner face. This gives the whole cone a brown color and a densely hairy appearance. It would seem impossible for the cone to be wetted by rains. The changes in temperature in this region are so slight that the hairy condition could hardly be related to this factor.

The lower greenish sporophylls never bear ovules or even primordia of them. The next sporophylls have occasional primordia, but it is only when the larger sporophylls are reached that normal ovules appear. Even the uppermost sporophylls bear ovules which sometimes ripen into seeds. The uppermost sporophyll is almost circular in transverse section. Its two ovules usually abort, as do those of the next sporophyll below it, but from this point, down to the sterile sporophylls at the base of the cone, each sporophyll bears two ovules which may develop into seeds. The ovules in a cone number about 100–300, and probably 200 ripe seeds is a liberal estimate for the larger cones. Where plants are isolated and pollination is uncertain, there are few ripe seeds, or even none at all. It would not be safe to say that the ovules of Dioon do not attain their full size unless pollination has taken place, for it is well known that the ovules of

FIG. 4.—Ovulate sporophyll, back and side view. ×½.

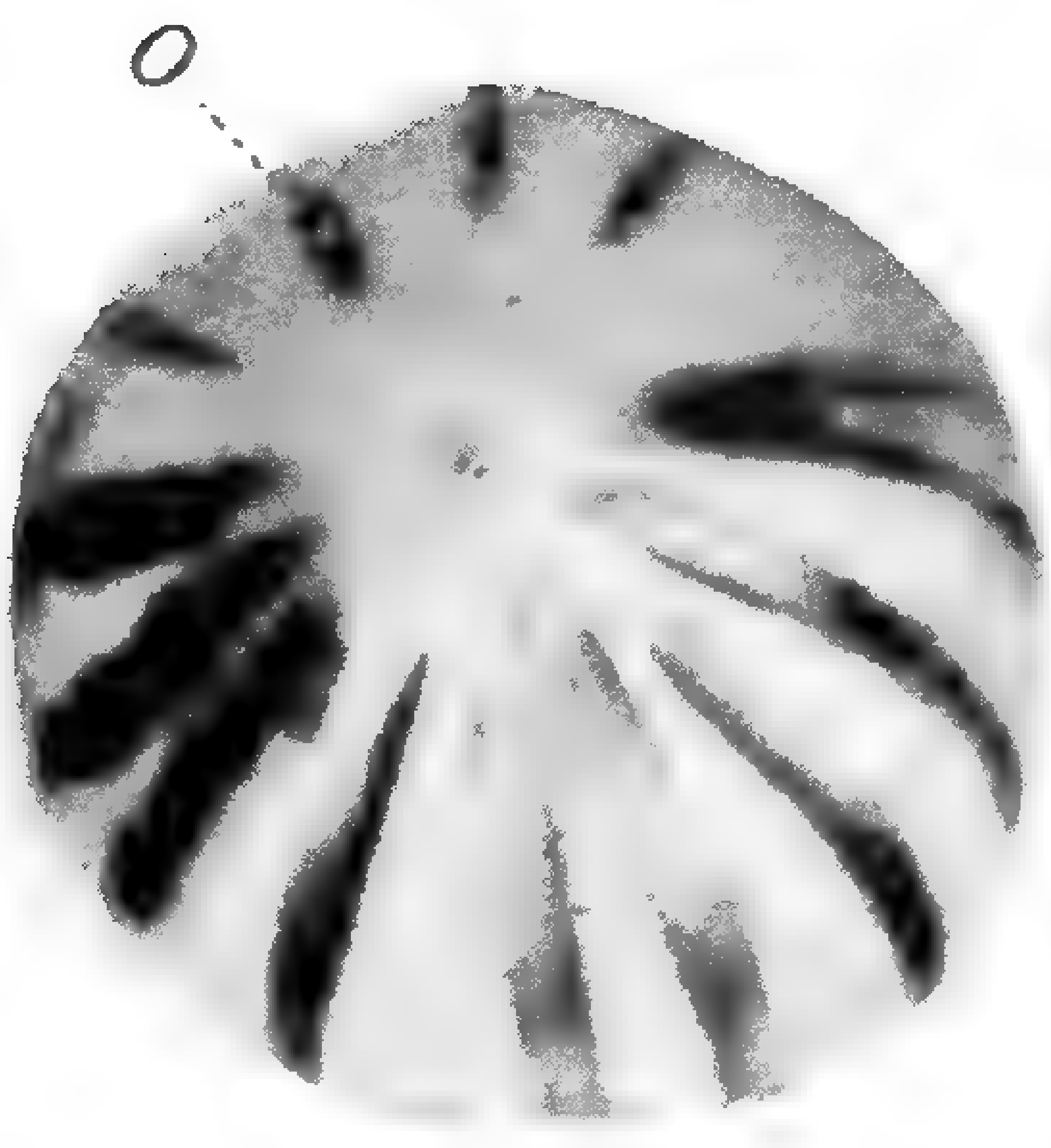
FIG. 5.—Ovulate sporophyll, inside view; ovules sessile. ×½.

FIG. 6.—Ovulate sporophyll, abaxial side; one ovule with pseudo-stalk, the other sessile. ×½.

other cycads reach their full size without the stimulus of pollination. However, the only greenhouse cone of Dioon which has come to my notice had only abortive ovules, and in the field the ovulate cones at any considerable distance from staminate plants are likely to contain only abortive ovules. Such ovules have not been pollinated. In cones bearing ripe seeds the abortive ovules have usually been pollinated, but have failed to develop from lack of room or of nutrition. It is easy to determine whether pollination has taken place, since the course of the pollen tubes is marked by conspicuous brown lines upon the nucellus.

The youngest ovules secured in 1904 were sent from the field November 1. These were 1^{cm} in length and showed the archegonium initials. Only one small cone had ovules as young as this, the ovules in other cones of this date measuring 1.5^{cm} in length and showing the central cell of the archegonium. November 14, six weeks after pollination, the average length of the ovules is about 2.3^{cm}; in the following spring (April 3), when the ovules had reached their full size, the largest ones measured 4^{cm} in length and 2.2^{cm} in diameter. The average length is about 3^{cm}, and the diameter 2^{cm}. Many ovules are nearly spherical, measuring about 3^{cm} in length and 2.8^{cm} in diameter. The ovules are perfectly smooth, and until nearly ripe are white, but become cream-colored or yellowish when exposed to the air; at maturity they have an orange color which contrasts sharply with the pale yellow of the naked portion of the sporophyll. They are sessile, but many of them appear to be stalked because strains due to the growth of the sporophylls and ovules draw out the base of the sporophyll into a stalk-like structure (*fig. 5*).

The ovule of Dioon reaches its full size before the stony layer becomes hard enough to occasion any serious difficulty in sectioning. Median longitudinal sections 3 or 4^{mm} in thickness, well dehydrated and cleared, but not stained, are best for a study of the general topography (*fig. 10*); while fresh ovules whose bundles have taken up eosin are most convenient for tracing the vascular system (*figs. 7, 8, 9*). The epidermis is smooth, strongly cutinized, and contains no stomata. At the base of the ovule the abscission layer is marked by a distinct constriction (*fig. 10, a*). The opening of the micropyle is amber or brownish in color from the drying of the pollination drop which, judging from the caliber of the micropyle, must be quite large, although it was not observed directly. Early in November the various tissues of the ovule are recognizable, and early in December the layers of the integument are almost as distinct as in the following March, although the cells of the stony layer have not begun to thicken, and microtome sections of the entire ovule can still be cut. The general topography of the ovule, as it appears later in December, is shown in *fig. 10*. In this figure the endosperm and fleshy tissues are dotted, the stony layer is more deeply shaded, and vascular bundles are represented by dark lines. The integument conists of three layers,



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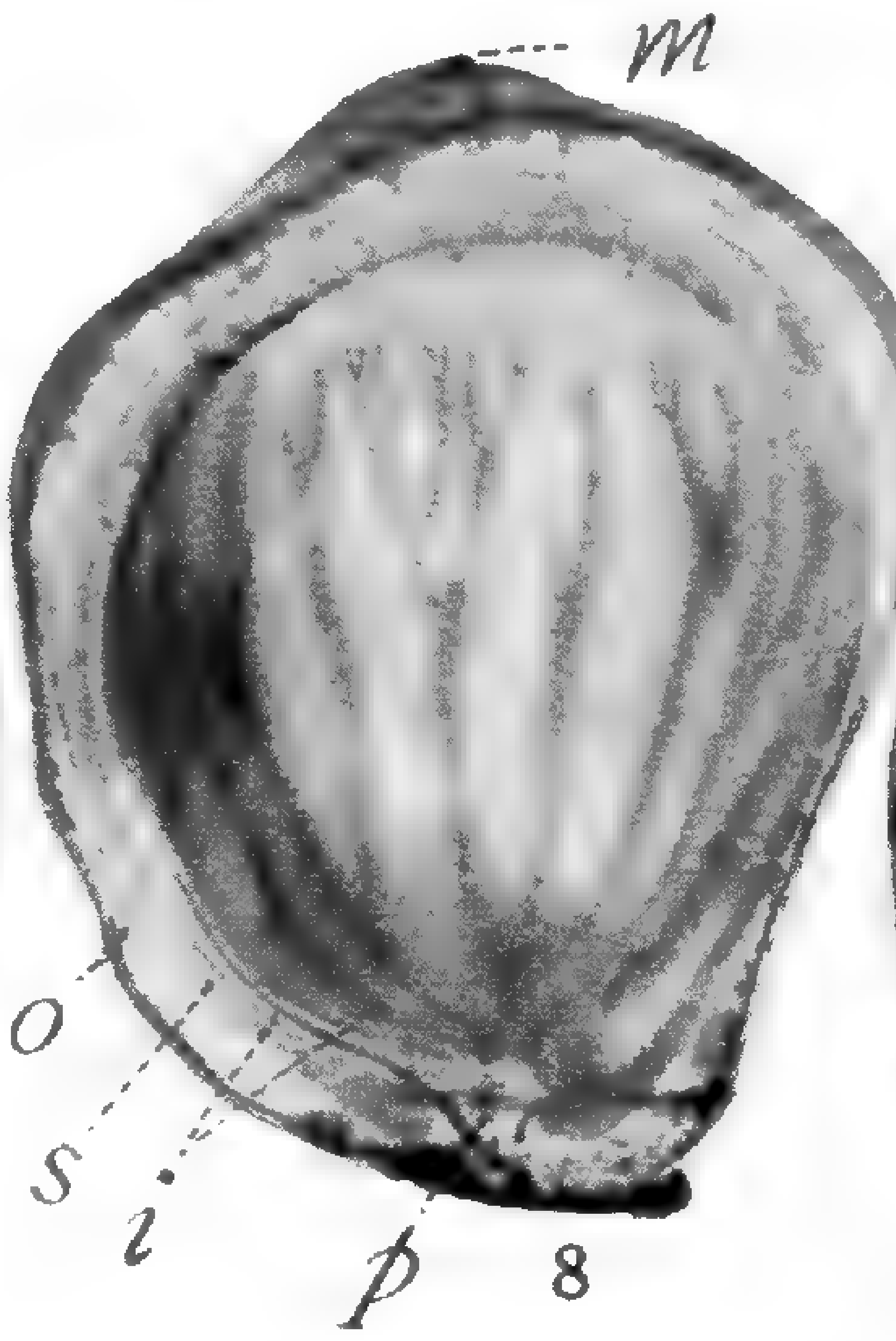

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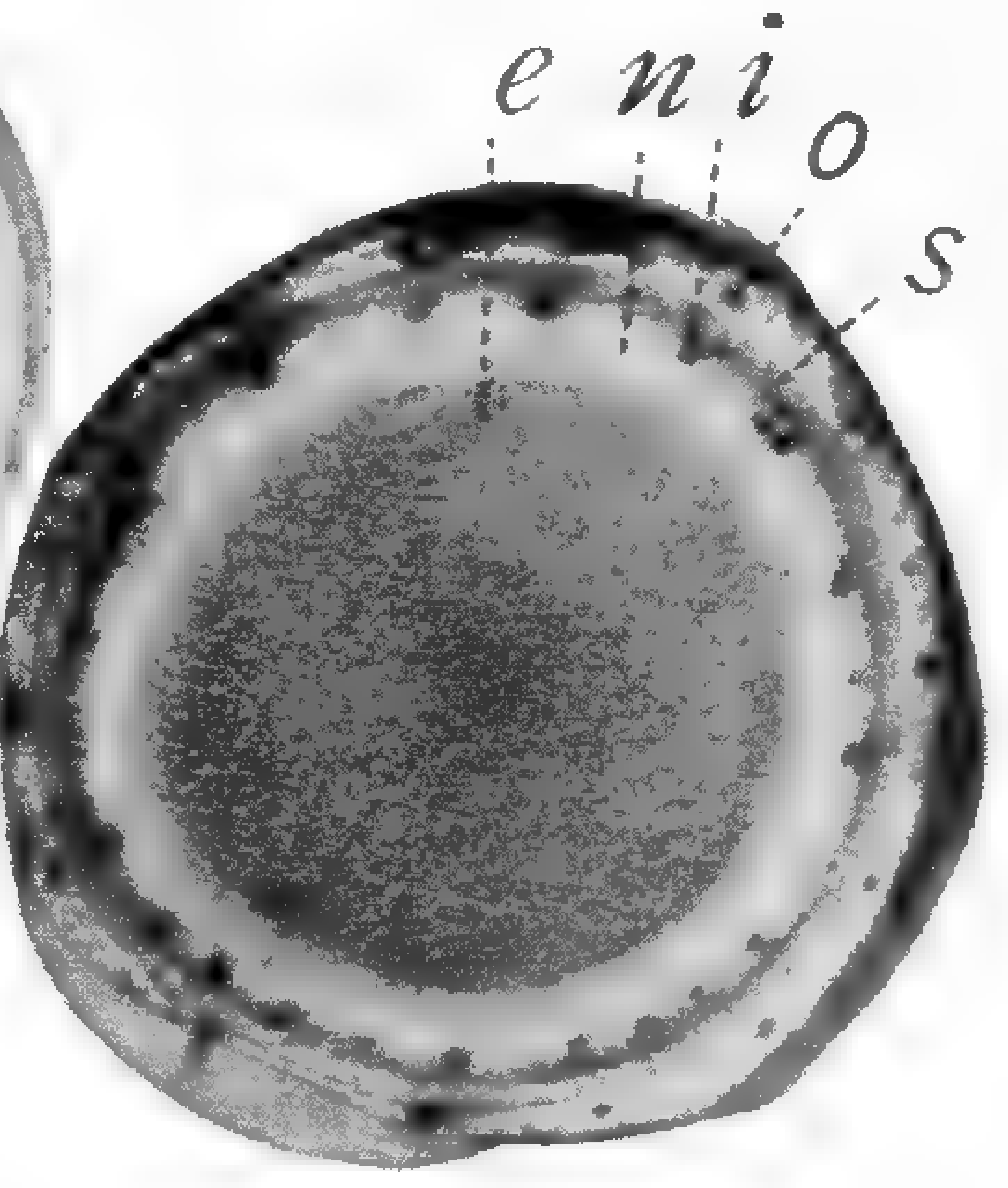

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FIG. 7.—Ovule photographed from above; the eosin has spread and exaggerated the size of the outer bundles (*o*). ×2.

FIG. 8.—Inner vascular system of ovule, treated with eosin and photographed after the endosperm and part of the inner fleshy layer had been removed: *i*, bundles of inner vascular system; *m*, micropyle; *o*, bundle of outer vascular system; *p*, basal papilla; *s*, stony layer. ×2.

FIG. 9.—Transverse section of ovule treated with eosin: *e*, endosperm; *i*, bundle of inner vascular system; *n*, inner fleshy layer of integument and fused portion of nucellus; *o*, bundle of outer vascular system; *s*, stony layer. ×2.

an outer and an inner fleshy layer, with a stony layer between them. Only a small portion of the nucellus is free from the integument. The fleshy layers of the integument are comparatively simple in structure.

The outer fleshy layer.—The outer layer at the stage shown in *fig. 11* is not sharply marked off from the stony layer. These two layers cannot be split apart, and even as late as May, when the stony layer has become very hard, the fleshy layer cannot be peeled off; it is only after it has become somewhat dry that it can be peeled off from the stony layer. However, the two layers easily separate as early as December if an ovule is cut in two and then allowed to decay for a few days in a damp atmosphere. The walls of the epidermal cells are considerably thickened and the outer surface is strongly cutinized. Most of the cells of the two layers just beneath the epidermis contain tannin, which occurs in only less abundance down to the level of the outer bundles. The cells containing tannin lie mostly in rows extending in the same general direction as the bundles. The large mucilage canals lie between the bundles and also have a general vertical course, but they branch and sometimes anastomose, so that some transverse sections of the canals are found even in longitudinal sections of the ovules. Beyond the zone of the bundles is a region of parenchyma cells (*fig. 11, p*).

The stony layer.—This layer, except at the deep pit which is occupied by the basal papilla, is thickest at the base and thinnest at the extreme apex. From the thin spot at the apex down to the lower part of the free portion of the nucellus it is thicker than throughout the middle two-thirds of the ovule. While the stony layer of the ripe seed is extremely hard, it is tougher and more elastic than the stony coat of most nuts, doubtless due to its complicated structure. The outer cells of the layer are small and isodiametric (*fig. 11, i*). In November they are not very sharply marked off from the inner cells of the outer fleshy layer; in fact, it is only after the walls of the stone cells have begun to thicken that the boundaries of the layers can be determined with accuracy. Beyond the small isodiametric cells is an irregular zone of cells elongated in a more or less longitudinal direction (*fig. 11, e*); then follows a zone of similar cells elongated transversely (*fig. 11, et*); and finally another zone of cells considerably elongated longitudinally (*fig. 11, i*). As growth continues, the small outer isodiametric cells simply increase in size and their walls became thickened. In the cells of the other three regions there is not only an increase in size and a thickening of the walls, but various displacements occur, so that the structure in March is much more complicated than in the preceding November. The elongating cells become crowded and interlaced and sometimes even branch, thus giving rise to an extremely tenacious tissue,

The inner fleshy layer.—This layer contains the inner vascular system, but otherwise consists of rather uniform, slightly elongated parenchyma cells. The cells are smaller than those of the main body of the nucellus, but there is no definite boundary between them. The boundary between the inner fleshy layer and the stony layer is less indefinite, and as early as January the two layers may be peeled apart, though with a rather uneven break. In small November ovules the inner fleshy layer has about the same thickness as the stony layer, but from this time the fleshy layer grows more rapidly, and in early December ovules is much thicker than the stony layer (*fig. 10*). The rapidly growing endosperm then begins to encroach upon the adjacent cells, which we regard as nucellar tissue intimately united with the inner fleshy layer of the integument, although it must be admitted that the ontogeny shows no indication of such a union. The encroachment continues until in the ripe seed all the tissues between the endosperm and the stony layer is reduced to a thin dry membrane, which peels off easily and cleanly, and shows very clearly the distribution of the inner vascular system. The inner fleshy layer is to be regarded as belonging to the integument rather than to the nucellus, because it is continuous with the inner fleshy layer of the free portion of the integument; because the bundles which it contains often extend into the inner fleshy layer of the free portion of the integument but never into the free portion of the nucellus; because in half-ripe ovules the fused portion of the nucellus may be peeled away from the layer containing the inner bundles; and, still more important, because such a conclusion is warranted by a comparison of the cycad ovule with those of fossil gymnosperms.

The phylogeny of the three layers.—This is an interesting question. Has the single complex integument always been single, or does it represent two integuments which have become fused? This is a question to which no definite answer can be given, because the early development of the ovule has never received sufficiently careful study in any cycad. The early stages in the development of the integument are passed before the cone breaks through the scale leaves, and consequently no material is likely to be secured in greenhouses. In the field, where material may be abundant, it would be necessary to cut out the growing points of many plants to secure a few ovulate cones. And even then, judging from a slight examination of the ovule of Ginkgo, the integument of which also has two fleshy layers with a stony layer between them, we should be likely to find the integument arising as a single undifferentiated tissue. A study of the integument of Dioon after its various tissues have become somewhat differentiated also fails to give any definite evidence as to its single or double nature.

I have been able to examine the integuments of several other cycads, but even where the differentiation between the layers is sharp, as in *Zamia integrifolia*, where the outer fleshy layer in both its cell-structure and cell-contents is sharply marked off from the stony layer, and where the differentiation between the stony layer and the inner fleshy layer is also rather distinct, there is no satisfactory evidence that the integument has ever been anything but a single structure. In Ceratozamia the layers are even less defined than in Dioon.

Judging from the literature of the subject, especially from the work of Miss STOPES (**16**), who has made the most thorough investigation, no study of the integument of living cycads can yield conclusive evidence as to its single or double nature. However, a comparison of the cycad ovule with that of the fossil Lagenostoma lends much strong support to the theory that the cycad integument is a double structure. OLIVER and SCOTT[13] suggest that the cupule of Lagenostoma is equivalent to the outer fleshy layer of the cycad integument, while the canopy of a Lagenostoma may have become simplified into the stony layer of the cycad seed. Miss STOPES' opinion is indicated by the title of her recent paper "On the double nature of the cycadean integument."[16] She believes that the plane of fusion between the two coats is either between the inner and outer portion of the stony layer or between the stony layer and the inner fleshy layer. The outer fleshy layer and the outer portion of the stony layer she believes to be too intimately connected to be separated morphologically. The structure of the Dioon integument, as it appears in sections, would seem to indicate that the plane of union has been between the inner and outer layers of the stone (*fig. 11, et, i*). The integument of Ceratozamia would bear a similar interpretation; but in *Zamia integrifolia* the outer fleshy layer is so sharply marked off from the stony layer that one could easily regard the former as an adnate cupule equivalent to the free cupule of Lagenostoma. In spite of the close morphological continuity between the stone and the outer flesh during the early development of the integument of most cycads, the two layers separate readily at maturity. The carpels of syncarpous ovaries of angiosperms become so closely united that the planes of fusion seem completely obliterated and the tissues appear perfectly continuous, but at maturity the carpels separate along the original planes of union. Hence the close continuity of the tissues should not exclude the view that the outer fleshy layer of the cycad ovule represents a structure which has become adnate to the stony layer. On the other hand, the ready separation at maturity must not be urged too strongly as an argument in favor of a union at this plane, because at maturity the inner fleshy layer of all the cycads also separates just as readily from the stony layer, and the inner fleshy layer of the integument never separates at all from the lower portion of the nucellus. While it must be confessed that the cycadean integument itself offers no conclusive evidence of a double nature, we agree with Miss Stopes that it possibly represents a double structure. In regard to the plane of fusion we could not agree with her, but think it more probable that the union has taken place between the outer flesh and the stone.

The nucellus.—The nucellus is free from the integument only for a short distance, the free portion extending little beyond the top of the endosperm. The free surface is cutinized and the epidermal cells contain tannin. When very thick sections are cleared in xylol, the free portion is limited by a very conspicuous black line. The sharp beak closes and hardens immediately after pollination, imprisoning the pollen grains in the pollen chamber. After pollination the upper portion in the surface of the nucellus soon becomes marked by brown lines caused by the haustoria of the pollen, which never penetrate deeply, but lie just beneath the epidermis. In December a considerable mass of tissue separates the pollen chamber from the top of the endosperm, in which the archegonial chamber has not begun to form. Subsequent growth of the endosperm, together with extensive disorganization of nucellar tissue and also some enlargement of the pollen chamber itself, finally destroys all tissues between the pollen tubes and the archegonia. The mode of disorganization which results in the formation of the pollen chamber is easily seen. The middle lamella softens and breaks down, thus setting free a few cells which are soon resorbed, and so forming the beginning of a pollen chamber. The subsequent encroachment of the disintegrating region is most rapid downward, but is also increasingly extensive at the periphery, so that the completed chamber is more or less funnel-shaped.

Below the free portion of the nucellus its most conspicuous feature is the thick jacket which surrounds the endosperm (*fig. 11, ej*). This jacket is sharply differentiated from the rest of the nucellus, and is so tenacious that it can be stripped off with forceps. The megaspore-membrane sometimes adheres to it, but more often clings to the endosperm. Although the material contained no early stages in the formation of the jacket, it is evident that it originates as a layer only one cell in thickness. Where cells of the layer do not divide periclinally, it remains only one cell thick; if there is a single periclinal division, the layer becomes two cells thick; while another division would make it three cells in thickness. In the archegonial region a considerable portion of the cells undergo one periclinal division; while in the chalazal region nearly all the cells show such a division, and a large number undergo a second periclinal division. On the sides there is a gradation between these two extremes. The less prominent and less complete jackets of the Coniferales have been described by THOMSON (**21**).

The cells of the jacket are very frequently binucleate and occasionally three nuclei are found. In comparison with the size of the cell these nuclei are rather large, but their chromatin content is very scanty and the nucleoli are small (*fig. 12*). It is not at all uncommon in these cells to find a complete chromatic spirem lying perfectly free in the cytoplasm, with no trace of a nuclear membrane or any achromatic structures (*fig. 13*). In such cases the nucleolus is always present and is somewhat larger than that of resting nuclei. The amount of chromatin in the spirem is vastly greater than in the resting nuclei. This unique condition does not lead to the formation of daughter nuclei or even to the reorganization of the single nucleus, and the significance of the phenomenon is not evident. The cells of the jacket at this time are centers of extreme metabolic activity, all the materials for the nutrition of the rapidly growing endosperm passing through them, and in passing undergoing some change before reaching the endosperm. It may be that the peculiar nuclear condition is brought about by the extreme activity of the jacket cells.

The walls of the jacket cells are suberized and stain deeply with safranin, thus contrasting sharply with the cellulose walls on both sides of them. The most conspicuous cell contents are irregular granules and coarse strands, which stain so deeply with safranin that in a section of a November ovule the jacket appears as a bright red circle easily visible to the naked eye. The material of the granules appears very much like that of the outer part of the megaspore membrane, which THOMSON (**21**) found to be a suberized structure. He described similar granules in other cycads and found them to consist of amylodextrin, but in his form the amylodextrin disappeared before the stage represented in *fig. 13* was reached. (There are no pits in any of the cells of the jacket.) The irregular granules and strands adhere closely to the cell wall even after the cytoplasm has been drawn away by reagents, as shown in *figs. 12* and *13*. No granules or strands are found on the outer walls of the jacket cells or in the cells on either side of the jacket layer. The endosperm jacket differs decidedly from the archegonial jacket in having no pits in the walls; consequently, all substances must pass through the jacket by the usual method of transferring material from one cell to another.

The jacket is doubtless concerned with the nutrition of the structures within, like the jacket about the embryo sac of an angiosperm, the jacket about the seeds of gymnosperms, or the tapetum about the sporogenous cells of microsporangia. While the jacket in all these cases is concerned in nutrition, the mode of nutrition and the nature of it are different. It is most active while the endosperm is still spherical. As the endosperm elongates and approaches its full size, the jacket disintegrates, and at the stage shown in *fig. 10* it has broken up and only suberized fragments remain. As to its morphological nature, the jacket corresponds to the jacket or tapetum which surrounds the sporogenous tissue of microsporangia. In a microsporangium the jacket surrounds a large number of spores, while in the case under discussion it surrounds only one spore, which, at the stage shown in *fig. 10*, has developed an extensive prothallium. LANG (**12**), who secured early stages of this structure in Stangeria, describes an extensive sporogenous tissue in the ovule, and believes that the outer portion of it gives rise to the tapetum, while all the tissue within except the functional megaspore disappears. Unfortunately, no such early stages were secured in Dioon, but since the jacket surrounding the microspores may originate from either sporogenous or sterile cells, there seems to be no objection to regarding the jacket surrounding the megaspore as equivalent to that surrounding the microspores, especially since homosporous forms, to which all heterosporous forms must ultimately trace their origin, have well-developed jackets.

Base of the ovule.—The lower limit of the ovule is marked superficially by a slight constriction as soon as the abscission region begins to develop (*fig. 10, a*). This region does not extend straight across, but is depressed in the center, with the depression away from the body of the ovule. When the ovule breaks off, the slight protuberance at the base is due to the shape of the abscission zone. This zone, about twelve cells in thickness, consists of nearly isodiametric cells, and thus contrasts rather sharply with the elongated cells above and below (*fig. 14*). Almost as soon as the zone can be distinguished, intercellular spaces appear, which increase in size until they sometimes become as large as the cells themselves, making them appear somewhat like the stellate cells of Typha, Scirpus, and similar forms. These cells are rich in starch. Above the abscission region the axis of the ovule extends upward and terminates in a conspicuous projection which occupies a deep pit in the stony layer. This projection, which was described as the *Einstülpung* by Miss STOPES (**15**), may be called the basal papilla (*fig. 10, p*). In the unripe seed the tissue of the basal papilla is noticeably tougher than that of other portions of the outer fleshy covering. In the ripe dry seed it looks for a time like a toothpick broken off in the stony layer, but it soon decays like the rest of the fleshy layer and its place is marked by a conspicuous pit about 2^{mm} in diameter and extending almost through the stone. Large elongated cells containing tannin are abundant on both sides of the abscission zone, but they do not extend into it. Several large mucilage ducts, which lie within the region occupied by the vascular bundles, reach almost to the top of the basal papilla. In the position and shape of the abscission layer and also in the appearance of the basal papilla, Dioon resembles Lagenostoma as described by OLIVER and Scott (**13**) and illustrated in their *fig. 26*. The rest of the tissue on each side of the abscission zone consists of large, elongated cells, forming a loose parenchyma with irregular intercellular spaces like those of the abscission zone, except that the spaces are larger.

Vascular system of the ovule.—The distribution of the vascular system is easily traced by cutting off the petiole of the sporophyll under water and placing the cut end in an aqueous solution of eosin. The vessels become filled with the solution in a few minutes. For studying the course of the bundles in the ovule itself, it is better to cut the ovule just below the abscission layer. While the fluid does not always penetrate the ultimate tracheids, the course of the bundles is sharply marked, as may be seen in *figs. 7–9*, which are photographs of ovules treated in this way. For studying the transverse distribution of bundles, series may be obtained very rapidly by cutting sections of ovules treated with eosin and simply placing the sections in order upon a sheet of paper. The abundant mucilage causes them to adhere firmly, and the bundles appear as bright red dots.

A transverse section of the petiole of the megasporophyll near the axis of the cone shows about seven bundles, arranged in a straight line. Two of these bundles, one at each end of the row, are usually larger than the others, and develop into the vascular systems of the ovules. The other bundles branch repeatedly, so that in the widest part of the lamina of the sporophyll a transverse section shows about thirty bundles, still arranged in one straight line. The outer bundle forks once as it passes to the ovule, so that a transverse section just below the abscission line of the ovule shows two bundles. From each of these two bundles a branch passes toward the outer fleshy layer of the integument, and another branch toward the inner fleshy layer, thus giving rise to an outer and an inner vascular system with the stony layer lying between them (*fig. 10*).

The bundles which supply the outer fleshy layer of the integument branch several times before they reach the level of lower limit of the stony layer, but from this point they extend to the micropyle with no branching at all (*fig. 7*). The number of these bundles in vigorous ovules varies from 10 to 17, with 14 as the most frequent number; in abortive ovules 12 and 13 are the most frequent numbers. In every cone there are some abortive ovules, and it may be that an inferior vascular supply has something to do with their failure to develop.

The bundles passing to the inner fleshy layer begin to branch a little higher up than do those of the outer layer. There is some branching in the basal papilla; after passing out to the inner fleshy layer there is repeated forking, as shown in *fig. 8*, so that a transverse section taken at the level of the archegonia shows 40 to 60 bundles. After passing from the stony layer, these bundles run in the outer part of the inner fleshy layer of the integument and extend up to the free portion of the nucellus. Occasionally a bundle continues in the inner fleshy layer beyond the beginning of the free portion of the nucellus, but in no case was a bundle found entering the nucellus itself. Occasionally a small bundle passes through the middle of the basal papilla, through the thin portion of the stony layer, and into the tissue at the base of the endosperm. The development of the bundles and the significance of the various details of the vascular system have not been attempted.

IV. THE FEMALE GAMETOPHYTE.

Stages showing the origin and early development of the female gametophyte were not secured. Since fruiting plants are comparatively rare, and since they cannot be distinguished from vegetative specimens until the cones are well started in their development, the earliest stages could be obtained only by a vandal-like mutilation of plants large enough to bear cones. The youngest ovules, collected early in November, were about 8^{mm} in length, and showed the archegonium initials. The gametophyte had become cellular throughout, no free nuclear portion remaining at the center. Only one small cone had ovules as young as this, the ovules in the cones of this date measuring about 1^{cm} in length and showing the central cell of the archegonium.

During November, December, and January the pressure exerted by the young gametophytes is remarkable. At a slight cut into the tough layer which is to become stony, a distinct snap can be heard, the cut gapes open, and the gametophyte protrudes. Later, when its cell walls have become firmer, the gametophyte retains its form when cuts are made into the stony layer. When an ovule in which the gametophyte is still spherical is cut through the middle, the gametophyte, as seen with the naked eye, has a beautiful, radiating appearance, looking somewhat like a transverse section of a twig with very fine and numerous medullary rays. Until late in December the endosperm is almost transparent, so that the young archegonia are easily seen and counted, even when the endosperm is removed entire. Ordinary newspaper print can be read through a section of endosperm 4^{mm} in thickness. At this stage the endosperm tastes sweet on account of the abundant sugar, but as soon as starch begins to form it takes on a translucent white color, and as the starch becomes abundant an opaque white. Even before the starch begins to appear, the endosperm commences to elongate, and in February has reached a length of 15^{mm} and a breadth of 10^{mm}. In April, when the endosperm has reached its full size, it is about 25^{mm} in length and 17^{mm} in breadth.

Early in December there not only is no archegonial chamber, but the top of the gametophyte containing the young archegonia is even elevated (*fig. 15*). In February the tissue at the rim of the elevation begins to grow rapidly, while the growth of the elevation itself is checked; consequently, the elevation soon becomes the bottom of the archegonial chamber (*fig. 16*). At the time of fertilization the archegonial chamber has reached a depth of 1 to 1.5^{mm} (*fig. 17*).

The megaspore membrane.—Early in November, while the endosperm is still spherical, the megaspore membrane is well developed. In fresh material one might easily mistake the endosperm jacket for the membrane, but the jacket is much coarser and can be stripped off entire with forceps. The membrane is comparatively delicate, but pieces several millimeters in length may be stripped off with forceps. When the nucellus is removed, the portion of the membrane covering the archegonia usually adheres to the nucellus rather than to the endosperm. The membrane is thinner at the apex and base of the endosperm than on the sides. In young ovules, with the endosperm still spherical, the greatest thickness of the membrane which was measured was 3μ at the apex, 3.1μ at the base, and 4.5μ at the sides. The average at this stage is about 3μ at the base and apex, and 4.1μ at the sides. In ovules whose endosperm has reached a length of 1.5^{cm}, but in which the archegonial chamber has not yet begun to form, the membrane is rather uniformly about 5μ in thickness. In germinating seeds in which the embryo is beginning to break the stony layer, the membrane reaches a thickness of 9–10μ, but the membrane is homogeneous, there being no differentiation into layers as in earlier stages.

The membrane clearly consists of two layers, which may be called the endospore and exospore (*figs. 12, 18*). The outer layer in young ovules is three or four times as thick as the inner, but in older ovules the difference is not so great. The inner layer seems perfectly homogeneous under the highest magnification. The outer layer, under moderate magnification, looks somewhat like the dense outer layer of the megaspore membrane of Marsilea; but with a Bausch and Lomb $\frac{1}{16}$ immersion and Zeiss oc. 12 the structure appears to be comparatively loose (*fig. 18*). The entire outer layer consists of club-shaped bodies. In other gymnosperms similar bodies have been described as prismatic, but in Dioon they really consist of a globular or ovoidal outer portion connected with the inner layer of the membrane by a stalk. In surface view these bodies are seen to be regularly arranged and to be quite uniform in size, the diameter of the head in November ovules being about 0.85 μ, and in the following February about 1 μ. As will be seen from the figure, the stalks form a comparatively open structure between the heads and the endospore. This open region appears as a nearly black line when seen in sections more than 1 or 2 μ in thickness, so that there seem to be three layers, the extra layer being only an optical effect caused by the stalk region.

The membrane covers the entire female gametophyte, but after the pollen chamber breaks through the base of the nucellus the portion of the membrane covering the archegonial chamber is ruptured, so that the two chambers form one continuous cavity. This cavity is moist, but is not filled with a liquid. Only a few chemical tests were made and the results agreed with those of THOMSON (**21**), who found the outer layer of the membrane to be suberized, while the inner layer iss uberized only where it is in contact with the outer layer. The inner portion of the inner layer, next the gametophyte, consists of cellulose. That the megaspore membrane is a vestige surviving from an ancestry which shed the megaspores seems too probable to be questioned. If it could be assumed that the ancestors of all the living cycads had megaspore membranes of equal thickness, and that in the surviving forms the membrane has been reduced uniformly in all genera, then the living genus with the thinnest membrane could be regarded as the farthest removed from its ancestry, and the genus with the thickest membrane would represent most nearly the ancestral condition. In spite of the uncertainty of such suppositions, it seems reasonable to regard a thick membrane as a primitive character, and while not conclusive evidence in itself, it deserves to be considered with other features in any discussion of the phylogeny of the cycads.

It would be interesting to know the thickness of the megaspore membranes of the other cycads at various stages in the life history. THOMSON (**21**) found that in *Cycas revoluta* the membrane is slightly more than 5μ in thickness at the stage when cell division is beginning in the endosperm. At a somewhat later stage the same writer found the membrane of *Stangeria paradoxa* to be 4.5μ in thickness, and the same thickness is given for the membrane of mature seeds of *Zamia integrifolia;* while in *Ceratozamia longifolia* the membrane is 4.5μ in thickness at a stage when the archegonia have been formed. In *Dioon imbricatum,*[2] before the appearance of archegonia, the thickness was 3.8μ. I have measured the membrane in the above genera, except Stangeria, and find only such slight variations from THOMSON'S figures as may be accounted for by slight differences in stages of development. The extreme thickness of the membrane in the germinating seed of Dioon so much exceeds any of THOMSON'S measurements that it would be interesting to know whether the membranes of other gymnosperms increase so much in thickness when the seeds germinate. The megaspore membrane of Dioon is as thick as that of any cycad, and consequently, so far as this one character is concerned, Dioon is as primitive as any member of the group.

Development of the endosperm.—Early in November, about two months after pollination, the endosperm has become cellular throughout. If one might hazard a guess at previous stages, the November condition looks as if the free nuclear condition had been succeeded by the formation of very large cells which had been divided repeatedly. At a stage when the archegonium initial is first distinguishable, the peripheral cells of the endosperm about half way between the archegonial and chalazal regions present the appearance shown in *fig. 19.*

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[2] This form is described by MIQUEL, in his *Prodromus Systematis Cycadearum* (1861), under *Dioon edule* Lindl., as *β imbricatum,* and is based upon leaf characters.

Except at its apex, the structure of the gametophyte is like that shown in this figure, a single layer of small peripheral cells being succeeded by layers of larger and larger cells. At the apex, where the archegonial initials are appearing, the single layer of small cells broadens rapidly into a lenticular group, from 7–10 cells in thickness. This group consists of about 200 cells, which are considerably smaller than those of the peripheral layer, as may be seen by comparing *figs. 19* and *23*, which are drawn to the same scale. The archegonium initials may be seen at the periphery of this group. At this stage, the cells of the gametophyte contain no starch or other food stuffs, the only visible contents being the nucleus, a scanty amount of cytoplasm, and the transparent cell sap.

Three weeks later, when the endosperm has reached a length of 15^{mm}, the cell contents seem to be just the same as before, no accumulation of foodstuffs being visible. Cell division has progressed rapidly, so that the row of four cells shown in *fig. 19, a,* is now represented by the two rows (sixteen cells) of *fig. 20, a.* Sections of the endosperm 4^{mm} thick, fixed in Flemming's solution early in December, appear somewhat darker in the region of the archegonia. In the chalazal region there is also a slightly darker color. Microtome sections show that the color is due in part to occasional grains of starch, but more particularly to small globules, probably oil, which stain black with osmic acid. The fact that the cells are considerably smaller in the archegonial region also makes the endosperm appear denser at this place. In the ripe seed the gametophyte shows considerable differentiation (*fig. 21*). The cells of the peripheral layer are small, rich in protoplasm, and contain numerous very minute starch grains. This layer contrasts sharply with the next, the cells of which are much larger and contain larger starch grains. This second layer is in turn fairly well marked off from the rest of the gametophyte, which consists of still larger cells densely packed with large starch grains. Numerous isolated cells containing tannin form a broad zone midway between the center and periphery of the endosperm. The tannin is much more abundant in the upper part of the gametophyte.

Development of archegonia.—Probably all of the superficial cells of the group at the apex of the endosperm are potentially archegonium initials. The number of archegonia varies from none at all to ten. Several ovules at the period of fertilization showed no archegonial chamber and no trace of archegonia. Ten archegonia were observed in only a single instance, which was also exceptional in having two archegonial chambers. A single archegonium with a small archegonial chamber was observed in a few cases. Usually there are three, four, or five archegonia, with four as the most frequent number. An archegonium initial, which can be seen early in November, becomes distinguishable by its slightly greater size (*figs. 22, 23*). The division into a neck cell and central cell takes place early, probably in November (*fig. 24*). The neck cell divides almost immediately, forming the two-celled neck which is a constant feature in all cycads yet investigated. All December ovules not only showed the neck, but the neck had already divided into its two characteristic cells (*fig. 25*).

The central cell enlarges very rapidly, its scanty protoplasm forming a delicate layer pressed against the wall by the single large sap vacuole (*figs. 24, 25*). Even at the stage shown in *fig. 24*, the cells bordering upon the central cell are rather regularly arranged, and in *fig. 25* there seems to be a definite jacket. While this layer functions more or less in the nutrition of the central cell, the real archegonial jacket with its characteristic cell contents is formed later by both periclinal and anticlinal divisions in the jacket-like layer of *fig. 25*. The differentiation of the jacket is not so rapid at the apex of the central cell as at the sides and base. As soon as the jacket begins to be differentiated from the neighboring cells, the cytoplasm of the central cell increases rapidly, and soon the space which had been occupied by the single large vacuole is filled. The rapidly increasing cytoplasm shows a beautiful foam structure (*fig. 26*). At this stage there is no reticulum or even any fibers. The vacuoles of the central cell are much smaller at the apex and at its periphery than nearer the center. The walls of these vacuoles are themselves vacuoles, and there is a perfect gradation, so far as size and appearance is concerned, from the large vacuole near the center to the smallest vacuoles of the thin plates of cytoplasm which form the walls of the large vacuoles. Some of the walls of the larger vacuoles are shown in surface view in *fig. 26*, though most of the walls show only the edges, as in case of cell walls. The smallest of the vacuoles are small enough to come within BÜTSCHLI'S limit for the size of meshes of genuine protoplasmic structure. The central cell of the archegonium is formed early in November, a little more than two months after pollination. The mitotic division which gives rise to the ventral canal nucleus and the nucleus of the egg takes place about the middle of the following May, so that the growth of the central cell and its nucleus extends over a period of six months. Throughout this entire period the growth is uniform, there being no cessation or retardation as would be the case in a colder climate.

The nucleus of the archegonium initial begins to enlarge very early, and is noticeably larger than the nuclei of the surrounding cells as soon as the initial itself becomes distinguishable (*fig. 22*); but while the growth of the nucleus continues steadily, it does not keep pace with the more rapid growth of the central cell. In March, after five months growth, the diameter of the nucleus has increased from 10μ to 70μ. The nucleolus, which at first was inconspicuous, has become prominent, and the chromatin granules are evenly distributed throughout the nucleus. At this time several large nucleolus-like bodies appear in the cytoplasm near the nucleus (*figs. 27, 29*). These bodies strongly resemble those which are found between the blepharoplast and nucleus in the body cell of Gingko, as described by HIRASE (**9**). At first they are solid and perfectly homogeneous; but as the nucleus of the central cell begins to divide, they become vacuolate (*fig. 29*), and before the mitosis has reached the metaphase they have broken up into innumerable small globules and granules (*fig. 30*). These bodies stain black with iron haematoxylin, and with the safranin gentian-violet combination they usually take the violet even when nucleoli are staining red with the safranin. Their exact nature and function was not determined, but they do not seem to differ, except in size, from the globules of nutritive material which are soon afterward brought into all parts of the egg by the haustoria.

The ventral canal nucleus.—While the growth of the nucleus of the central cell extends over a period of more than six months, its division, when once begun, is extremely rapid. The only figures found were in material sent from Xalapa on April 1, 1905, and fixed at Chicago on April 13 and 17. No figures were found in any of the numerous collections fixed in March. Some ovules fixed later than April 17, and even as late as May 13, showed the nucleus of the central cell still undivided; but such ovules were from cones picked about the middle of March, and the ovules finally decayed without any division of this nucleus. The top of the typical archegonium in such material is shown in *fig. 28*, which is from a cone picked March 18, the material being fixed May 13, nearly two months later. The two neck cells are in perfect condition, but the central cell has begun to degenerate.

In normal material the spirem is broad but very tenuous in consistency. In the only cases noted it had evidently suffered from reagents (*fig. 29*). The shortening, condensation, and segmentation of the spirem were not observed, the next available stage being shown in *fig. 30*, where the segmentation into chromosomes has taken place. The splitting of the chromosome in the equatorial plate is shown in *fig. 31*. In this preparation the number of chromosomes was determined with reasonable though not absolute certainty to be twelve. In a late anaphase the chromosomes, while still retaining the U-shape, are becoming irregularly moniliform, looking as if they might break up into small pieces (*fig. 32*). Only a few stages in the formation of the spindle were observed. The first indication of it is a granular and fibrillar appearance which is more marked at the lower pole of the nucleus (*fig. 29*). There are no centrosomes, and in *fig.* 30 the poles are rather blunt. Fibers like the spindle fibers are abundant in the cytoplasm of the papillate projection in which the figure lies. In *fig. 31* the spindle is more sharply bipolar, and long mantle fibers are more conspicuous, although many of the spindle fibers are still continuous from pole to pole. *Fig. 32* shows no trace of the granules which mark the beginning of a cell plate, and later stages make it certain that no wall is formed between the daughter nuclei. The ventral canal nucleus remains free in the cytoplasm of the egg, as shown in *figs. 33–35*.

A ventral canal cell in cycads was first described by **STRASBURGER** (**18**) in 1876 for *Cycas sphaerica*. The next year **WARMING** (**23**) described one in *Ceratozamia robusta*, but soon concluded that he had been mistaken. **TREUB** (**22**) in 1884 failed to find any ventral canal cell in *Cycas circinalis*, and from that time it was generally believed that the cycads have no ventral cell. However, in 1898 **IKENO** (**10**) made an unmistakable demonstration of the critical mitosis in *Cycas revoluta*. At that time no ventral canal nucleus not separated from the egg nucleus by a wall had yet been observed, and he merely followed current terminology. The term ventral canal nucleus was introduced by COKER (**3**) in 1902 to describe the condition in Podocarpus. IKENO'S figures show that no wall is formed between the ventral canal nucleus and that of the egg. WEBBER (**24**) soon afterward reported that in Zamia "a small cell is cut off at the apex of the archegonium," but here too the language is unfortunate, for no cell is cut off, and the ventral canal nucleus remains in the general cytoplasm of the egg, as shown by COULTER and CHAMBERLAIN (**5**). I have recently made preparations of Encephalartos showing the same condition. It is probable that no ventral canal cell is cut off in any of the cycads, there being merely a nuclear division.

It cannot be doubted that this represents an advanced stage in the reduction of the archegonium. It offers no exception to the method by which the row of neck canal cells of the bryophytes and pteridophytes has been reduced. In these groups binucleate neck canal cells are frequent. This means that the formation of a cell wall has failed to follow the nuclear division. The next stage in reduction would be the suppression of the mitosis, and thus a diminution in the number of neck canal cells. In this way the neck canal cells gradually become reduced in number, some pteridophytes showing only a single one. In gymnosperms there is no neck canal cell at all, and the ventral canal cell is being eliminated by the same process. In some genera, like Pinus, the ventral canal cell is separated from the egg by a wall. In other genera the nuclear division takes place, sometimes with a series of granules on the spindle indicating a rudimentary cell plate, but no wall is formed. In Torreya it seems likely that even the ventral canal nucleus is suppressed. The absence of a ventral canal nucleus has been reported for several genera, but the evidence is not conclusive. Dioon, Zamia, Cycas, and Encephalartos still preserve the mitosis, although the wall is no longer formed. In this particular, although the oldest of living gymnosperms, the cycads do not show as primitive a condition as do Pinus and some other Coniferales.

After the mitosis described above, the ventral canal nucleus forms a membrane and may enlarge slightly, but it soon disorganizes, so that at the time of fertilization a scarcely recognizable vestige remains.

Typical views are shown in *figs. 33, 33a,* and *34.* Occasionally there is considerable enlargement (*fig. 35*), as is often the case in Pinus. I have a preparation of Encephalartos which not only shows a reorganization and enlargement of the ventral canal nucleus, but the nucleus has moved down from the papillate projection toward the egg, suggesting the possibility of fertilization of the egg by the ventral canal nucleus. In STRASBURGER'S account (**33**) of fertilization in *Picea vulgaris* and in COULTER'S account (**3**) in *Pinus Laricio*, describing fusing nuclei of equal size, a large ventral canal nucleus was doubtless mistaken for a male nucleus, but that these were actual cases of fertilization of the egg by its own ventral canal nucleus there can be but little doubt.

The egg and archegonial jacket.—The egg of Dioon is the largest yet known in plants. It is seldom less than 4^{mm} in length and often reaches a length of 5^{mm}; the largest egg measured was 6^{mm} in length. The actual size, just after the formation of the ventral canal nucleus, is shown in *fig. 17a.* The egg at the right in this figure is shown again in *fig. 17*, which is magnified six diameters so as to show the comparative size of the papilla, ventral canal nucleus, and egg nucleus. Before fertilization the egg nucleus becomes much larger and more deeply placed than is represented in this figure. In *fig. 15*, which shows the actual size of the central cell before the beginning of the archegonial chamber, and in *fig. 16*, showing the beginning of the archegonial chamber, the nucleus of the central cell is too small to be represented even by a single dot.

The nutrition of the egg is practically the nutrition of the central cell, for it reaches its mature character before the mitosis which separates the ventral canal nucleus from that of the egg. GOROSCHANKIN (**8**) in 1883 described a continuity of protoplasm between the jacket cells and egg of Ceratozamia. He believed that strands of protoplasm pass through sieve plates in the pits of the jacket. IKENO (**10**) in 1898 made a more detailed study of the growth of the egg in Cycas. He also described protoplasmic continuity between the jacket cells and the egg, and a passage of proteid materials from the jacket into the egg. Miss ISABEL SMITH (**14**), who studied the nutrition of the egg in *Zamia floridana*, found no connecting strands of protoplasm, but found projections, which she called haustoria, extending from the egg into the jacket cells. In Dioon there are haustoria similar to those of Zamia. An examination of Ceratozamia, Cycas, and Encephalartos showed that they also have haustoria like those of Zamia and Dioon. The origin, development, and function of the haustoria, together with changes in the jacket cells of the surrounding tissue, would be a long problem, involving chemistry as well as morphology.

During the early stages of its growth (*figs. 24–26*) the central cell receives food material from the surrounding cells by the usual method of transferring substances from one cell to another. Up to the stage shown in *fig. 25*, the wall of the central cell is very thin, with no visible pits; but later the inner surface of the wall undergoes an extensive secondary thickening, interrupted only by the large pits which are such a conspicuous feature of cycad eggs. After the haustoria have become fully developed, their cytoplasm is in direct contact with that of the jacket cells, so that substances may pass from the jacket cells into the haustoria as readily as from one part of the jacket cell to another. A paper was received from Drs. STOPES and FUJII (**17**) just as this account is going to press, describing sieve plates as found by GOROSCHANKIN (**8**). Their figures are evidently drawn from young material, in which the haustoria have not reached their full development. That there is protoplasmic continuity here, as elsewhere, we do not doubt; but if the pit-closing membrane persists in stages like those shown in our *figs. 37–41*, it has escaped our observation. The haustoria project far into the cells of the jacket, and the mere thrust may have ruptured the membrane. At the stage shown in *fig. 36*, it is possible that the membrane may still be present; but in stages like *figs. 37–41* we could not find any membrane, even after a reexamination of our preparations. Consequently, we see no reason for modifying the following account, which was written before the paper by Drs. STOPES and FUJII was received.

The general method by which nutritive materials reach the egg is easily understood. The tissue of the female gametophyte is filled with starch and other food materials, which in a changed form pass into the archegonial jacket and thence into the egg. The cells of the archegonial jacket at certain times contain numerous starch grains, much smaller than those in the surrounding endosperm cells, but the starch is soon dissolved. The change from starch to a soluble form doubtless takes place repeatedly, because the starch at various stages in the development of the archegonium is sometimes present and sometimes absent. The protoplasm of the jacket cells is abundant and their nuclei are much larger than those of the surrounding tissue. The changes taking place within these cells and nuclei resemble those which occur in glandular cells, there being a period of accumulation, followed by discharge, and then exhaustion, after which the processes are repeated. Glandular activity begins in December, as soon as the archegonial jacket becomes distinguishable. At this time the protoplasm of the central cell consists of a thin peripheral layer, and still thinner lamellae which divide the interior into vacuoles of various sizes, those near the center being the largest (*fig. 36*). The activity increases gradually up to the time of fertilization, about the first of May, and then diminishes. At the close of the period of free nuclear division in the proembryo, the jacket is not very vigorous, but there is still some activity. Toward the close of the intrasporal development of the proembryo, the jacket cells become weak in contents and begin to break down; and after the embryo has broken through the base of the egg and advanced 4 or 5^{mm} into the endosperm, the jacket is scarcely recognizable. During the period of repose or exhaustion (*fig. 36*) the protoplasm of the jacket cells is finely vacuolated. The nucleus has a somewhat homogeneous, finely granular structure, in which the chromatin is not conspicuous, although it can be seen that most of it is in the half of the nucleus nearest the egg. The protoplasm of the haustoria is evenly granular.

As activity begins (*fig. 37*), the protoplasm of the jacket cells becomes more coarsely vacuolated and food materials of various shapes and sizes appear within it. The nucleus is particularly active. The nucleolus becomes saturated with a substance which stains black with iron haematoxylin, and the chromatin first becomes conspicuous and then obscured by a substance which also stains black and may be the same as that in the nucleolus. Material passes from the nucleus into the cytoplasm and from the cytoplasm into the haustoria. Once within the haustoria, the food materials are already within the egg. In passing from the haustoria to the deeper portions of the egg, the materials break up into smaller and smaller granules and globules, so that the periphery of the egg always contains the most conspicuous contribution from the jacket. The food materials never take the form of "proteid vacuoles" as in Pinus, and are never in danger of being mistaken for nuclear structures. The appearance of the jacket and the periphery after a discharge is almost completed is shown in *fig. 38*.

The three preceding illustrations (*figs. 36–38*) show the conditions in young eggs while the protoplasm is still quite scanty, most of the space being occupied by large vacuoles. Later stages, after the egg has become filled with protoplasm and the large vacuoles have disappeared, are shown in *figs. 39–41*. In *fig. 39* the ends of the haustoria are covered by a frothy substance, and in *fig. 40* it is seen that this substance is passing into the egg. A large vacuole marks the place which has just before been occupied by frothy substance. The nucleus, as is often the case, is concave on the side next the haustoria. A later stage is shown in *fig. 41*, which represents various kinds of food materials within the egg. Globules and droplets of various forms are most abundant, but crystalloids are not infrequent. The crystalloids are cubical or may approach the spherical form, but are never fusiform like those so characteristic of the egg of Zamia. Starch is sometimes present but generally absent.

The structure of the protoplasm of the egg undergoes great changes, especially during the last two months of its development. In December the protoplasm, containing one large vacuole, forms only a thin layer pressed against the periphery of the central cell (*fig. 25*). In March the protoplasm has increased greatly in quantity and numerous vacuoles have appeared (*figs. 36–38*). In these figures, and even in considerably later stages, the lines represent the edges of lamellae, and the appearance is a strong argument in favor of the foam or *Waben* theory of the structure of protoplasm. In later stages, however, the foam structure disappears, and the protoplasm seems to be almost entirely in the form of fibrillae (*fig. 41*). The change seems due in great part to the breaking down of lamellae, thus leaving fibrillae at the junctions.

Why the nucleus of the central cell remains at the apex for so many months, and why after the mitosis the egg nucleus moves down while the ventral canal nucleus remains at the apex, are questions still unanswered. A moment's reflection will convince any one that neither temperature, light, nor gravity has any appreciable influence. The path by which nutrition reaches the egg may be an important factor, for the extensive vascular system of the ovule terminates near the top of the endosperm. On the other hand, the same position of the nucleus is found in gymnosperms whose ovules have scarcely any vascular tissue at all. Later, during the formation of the proembryo, the polarity is reversed, the nuclear activity being most vigorous at the base of the egg. At this time it is evident that nearly all the nutrition is coming from the endosperm at the base of the egg. As a working hypothesis it may be suggested that the early position of the nucleus at the apex, and also the reversal of the polarity, are due to chemotaxis, the source of nutrition being the controling factor.

The egg nucleus.—The egg nucleus of Dioon is the largest which has yet been found in plants. Its usual diameter is about 500 μ, but nuclei sometimes reach a diameter of 600 μ. Not infrequently the nucleus is elongated, and in such cases its bulk is likely to be greater than that of the usual spherical nucleus. One nucleus measured 1475 μ by 380 μ. In spite of the immense size of this nucleus, its structures could not be interpreted. Its chromatin content is shown at the lower end of the spindle in *fig. 32*. Stages immediately following this were not secured, and in stages like *figs. 34* and *35* the chromatin can no longer be identified. From this time to the entrance of the sperm into the egg, the internal structure of the nucleus is shown in *figs. 42–44*, which represent details as they appear under a magnification of 1300 diameters. The entire nucleus, drawn to this scale, would be more than 6^{m} in diameter! In all parts of the nucleus is found a delicate network of varying thickness, and upon it or imbedded in it are granules and globules of various sizes. The smallest granules, which are almost always associated with the network or clinging to the surface of larger globules, stain with gentian-violet. Most of the larger globules stain with safranin, so that the general tone of the network is red; but some stain with the gentian-violet and in others the two stains blend. There are always a few which do not stain at all. In most preparations the network stains very faintly or not at all. The nucleoli, which are large and vacuolated, can usually be distinguished from the globules represented in *figs. 42–44*. If any of these granules represent the chromatin, the individuality of the chromosomes would appear to be hopelessly lost. No satisfactory study of the living nucleus was made. A nucleolus is visible in living material, but otherwise the contents seem nearly homogeneous. There are few globules and the network could not be identified. It is possible that most of the globules and the network are coagulation artifacts due to fixing.

The development of the egg nucleus seems to be essentially the same in all gymnosperms. Among the investigators who have studied this nucleus in various gymnosperms may be mentioned STRASBURGER (**19**, **20**), IKENO (**10**), BLACKMAN (**1**), CHAMBERLAIN (**2**), FERGUSON (**7**), and LAND (**11**). BLACKMAN, CHAMBERLAIN, and FERGUSON attempted to follow the behavior of the chromatin, but the accounts are inadequate, there being stages in which all fail to identify convincingly the chromatin. Miss FERGUSON'S beautiful figures of Pinus show the familiar structures with great accuracy, but just what structures are chromatin is not clear. My own series of Pinus is less complete, and those of other writers are still more incomplete. In Dioon it is evident that this nucleus behaves much as in Pinus. The solution of the problem is not easily attained in cycads on account of the inaccessibility of material and the difficult sectioning. In Pinus, with its abundant material and easy technique, a close series in the development of the nucleus and in the formation of the spirem at the time of fertilization would probably lead to an understanding of the egg nucleus of the whole group.

SUMMARY.

1. Dioon occurs in abundance at Chavarrillo, Mexico.

2. It is probable that plants often reach an age of more than one thousand years.

3. The ovulate strobilus is more like the loose ovulate strobilus of Cycas than the compact ovulate strobili of the other genera.

4. The megasporophylls are more leaf-like than those of any other genus of cycads except Cycas.

5. The integument consists of three layers: an outer and an inner fleshy layer, with a stony layer between them. The integu-

ment is probably double in nature, the outer fleshy layer representing the outer integument.

6. Only a small portion of the nucellus is free from the integument.

7. One vascular bundle passes from the sporophyll toward each ovule. Before entering the ovule the bundle forks, one branch forming the continuously branching system of the inner fleshy layer of the integument, and the other forming the slightly branched system of the outer fleshy layer.

8. The megaspore membrane varies in thickness from 3–4.5 μ in young ovules to 9–10 μ in mature seeds.

9. The number of archegonia varies from one to ten, with four and five as the most frequent numbers. The archegonium initial appears in October; the division into neck and central cell takes place almost immediately after; the mitosis which forms the ventral canal nucleus and egg nucleus takes place during the next May.

10. The central cell and egg during earlier stages receive food substances by the ordinary method of nutrition, but later receive food material through haustorial projections from the egg which are in direct contact with the cytoplasm of the jacket cells.

11. There are twelve chromosomes in the egg nucleus, which is the largest one yet known in plants.

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LITERATURE CITED.

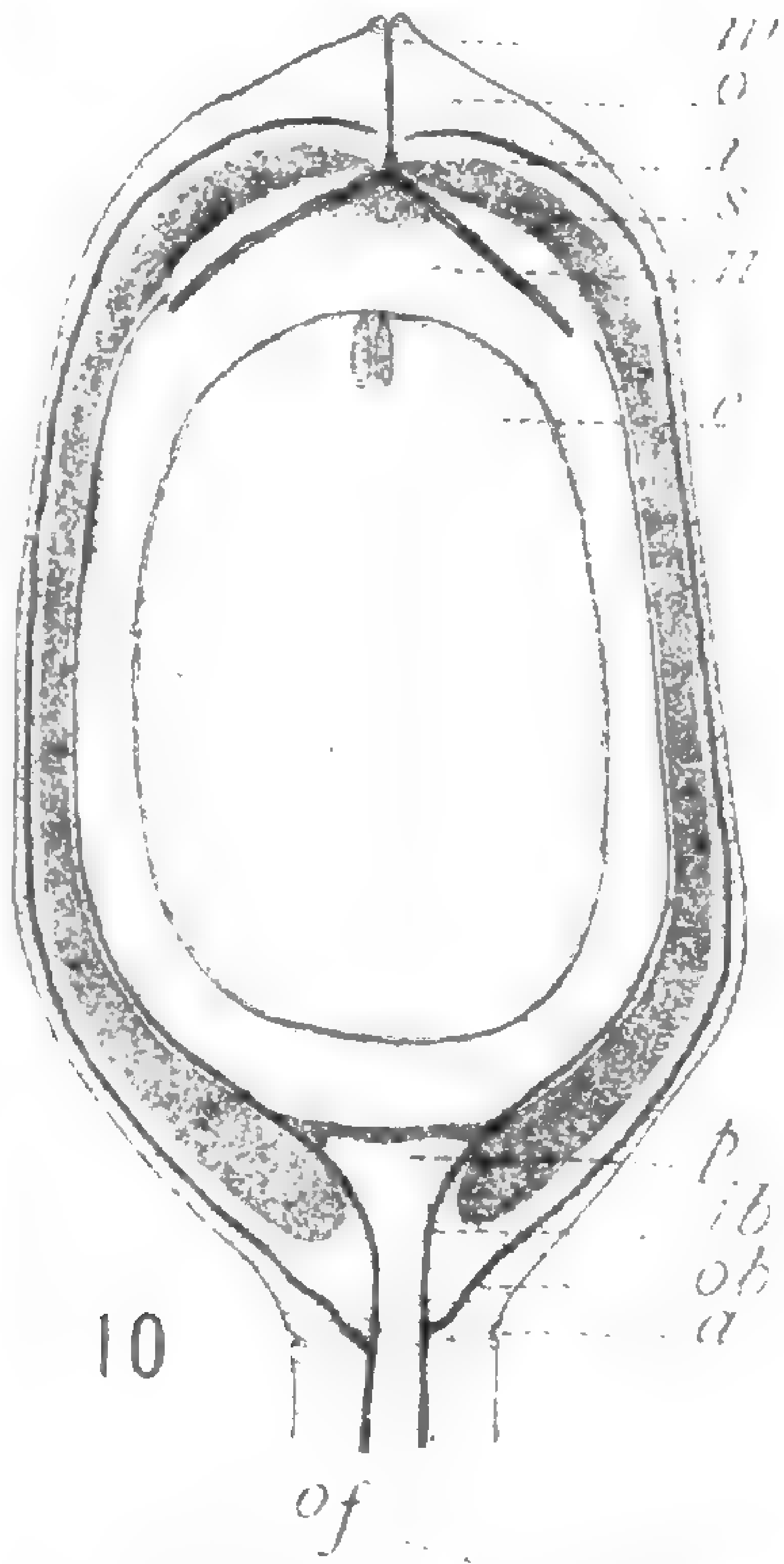
1. BLACKMAN, V. H., On the cytological features of fertilization and related features in *Pinus sylvestris* L. Phil. Trans. Roy. Soc. London B. **190**: 395–426. *pls. 12–14.* 1898.
2. CHAMBERLAIN, C. J., Oogenesis in *Pinus Laricio.* BOT. GAZETTE **27**: 268–280. *pls. 4–6.* 1899.
3. COKER, W. C., Notes on the gametophytes and embryo of Podocarpus. BOT. GAZETTE **33**:89–107. *pls. 5–8.* 1902.
4. COULTER, J. M., Notes on the fertilization and embryogeny of Conifers. BOT. GAZETTE **23**:40–43. *pl. 6.* 1897.
5. COULTER, J. M., and CHAMBERLAIN, C. J., The embryogeny of Zamia. BOT. GAZETTE **35**:184–194. *pls. 6–8.* 1903.
6. COULTER, J. M., and LAND, W. J. G., The gametophytes and embryo of *Torreya taxifolia.* BOT. GAZETTE **39**:161–178. *pls. 1–3.* 1905.
7. FERGUSON, MARGARET C., Contributions to the knowledge of the life history of Pinus. Proc. Wash. Acad. Sci. **6**:1–202. *pls. 2–24.* 1904.

8. GOROSCHANKIN, J., Zur Kenntniss d. Corpuscula bei den Gymnospermen. Bot. Zeit. **41**:825–831. *pl. 70*. 1883.
9. HIRASE, S., Études sur la fécondation et l'embryogénie du *Ginkgo biloba*. Jour. Imp. Coll. Sci. Tokyo **8**:307–322. *pls. 31–32*. 1895.
10. IKENO, S., Untersuchungen über die Entwickelung der Geschlectsorgane und der Vorgang der Befruchtung bei *Cycas revoluta*. Jahrb. Wiss. Bot **32**:557–602. *pls. 8–10*. 1898.
11. LAND, W. J. G., Spermatogenesis and oogenesis in *Ephedra trifurca*. BOT GAZETTE **38**:1–18. *pls. 1–5*. 1904.
12. LANG, W. H., Studies in the development and morphology of cycadean sporangia. II. The ovule of *Stangeria paradoxa*. Annals of Botany **14**: 281–306. *pls. 17–18*. 1900.
13. OLIVER, F. W., and SCOTT, D. H., On the structure of the paleozoic seed, *Lagenostoma Lomaxi*. Phil. Trans. Roy. Soc. London B. **197**:193–247. *pls. 4–10*. 1904.
14. SMITH, ISABEL, The nutrition of the egg in Zamia. BOT. GAZETTE **37**: 346–352. 1903.
15. STOPES, M. C., Beiträge zur Kenntniss der Fortpflanzungsorgane der Cycadeen. Flora **93**:435–482. 1904.
16. ———, On the double nature of the cycadean integument. Annals of Botany **19**:561–566. 1905.
17. STOPES, M. C., and FUJII, K., The nutritive relations of the surrounding tissues of the archegonia in gymnosperms. Beih. Bot. Centralbl. **20**: 1–24. *pl. 1*. 1906.
18. STRASBURGER, E., Ueber Zellbildung und Zelltheilung. Leipzig. 1876.
19. ———Befruchtung und Zelltheilung. Jena. 1878.
20. ———, Uber den Verhalten des Pollens und die Befruchtungsvorgänge bei den Gymnospermen. Hist. Beitr. **4**:1–158. *pls. 1–3*. 1892.
21. THOMSON, R. B., The megaspore membrane of the gymnosperms. Univ. Toronto Studies, Biol. Ser. no. 4. 85–145. *pls. 1–5*. 1905.
22. TREUB, M., Recherches sur les Cycadées. 3. Embryogénie du *Cycas circinalis*. Ann. Jard. Buitenzorg **4**:1–11. *pls. 1–3*. 1884.
23. WARMING, E., Recherches et remarques sur les Cycadées. Oversigter K. D. Vidensk. Selsk. Forh. 1877.
24. WEBBER, H. J., Notes on the fecundation of Zamia and the pollen tube apparatus of Gingko. BOT. GAZETTE **24**:225–235. *pl. 10*. 1897.

EXPLANATION OF PLATES XIII–XV.

(FIGS. 1–9 are text cuts.)

FIG. 10. Longitudinal section of ovule: *a*, abscission layer; *e*, endosperm; *i*, inner fleshy layer of integument; *ib*, bundle of inner vascular system; *m*, micropyle; *n*, free portion of nucellus; *o*, outer fleshy layer of integument; *ob*, bundle of outer fleshy layer; *p*, basal papilla; *s*, stony layer of integument. ×2.



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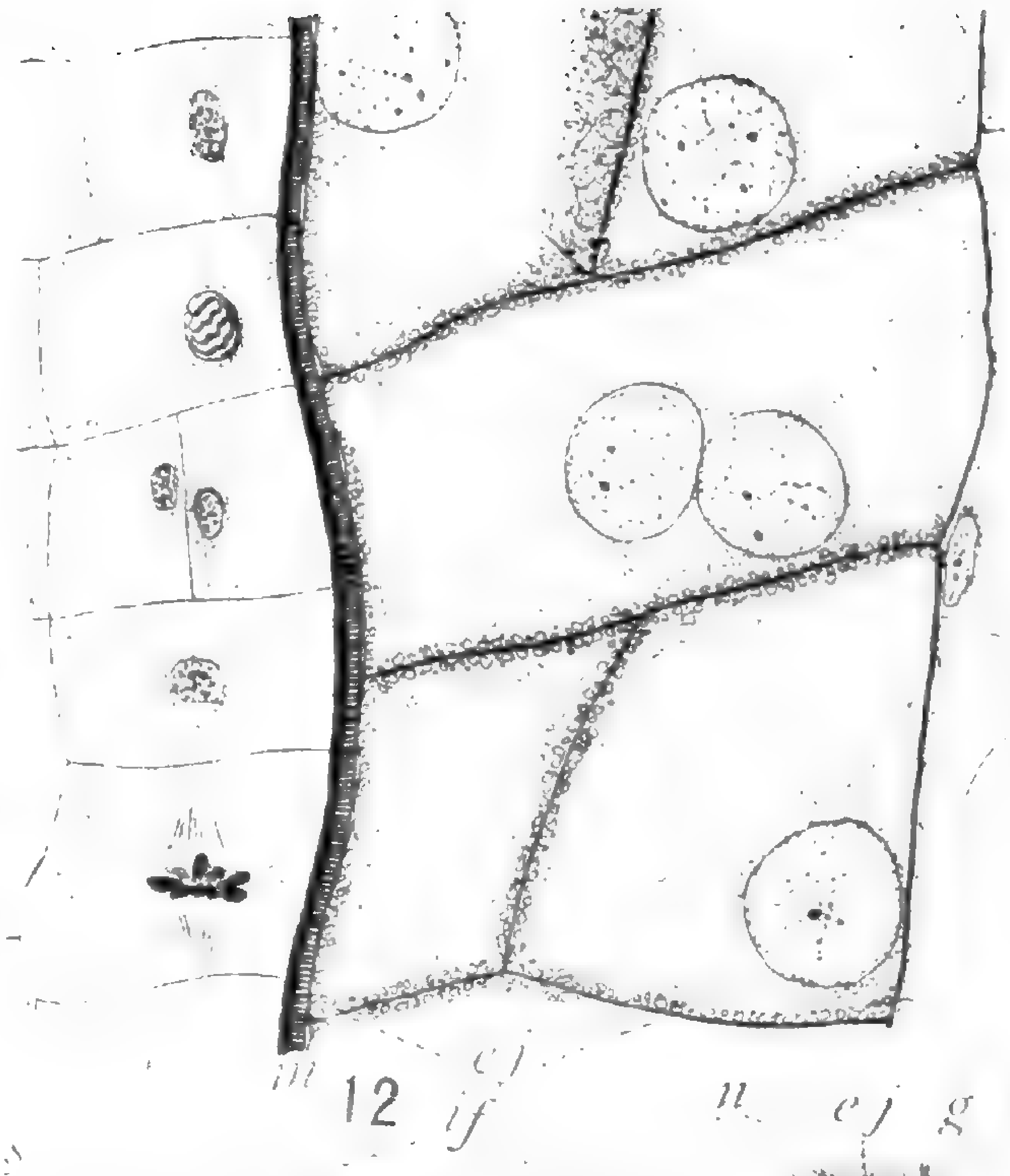

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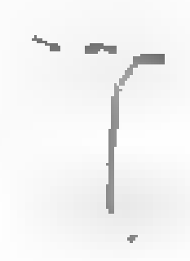

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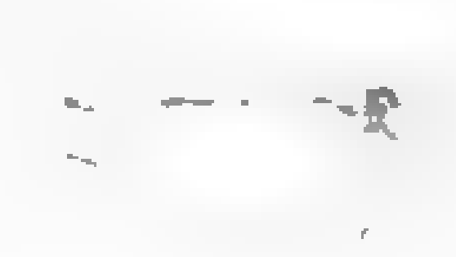

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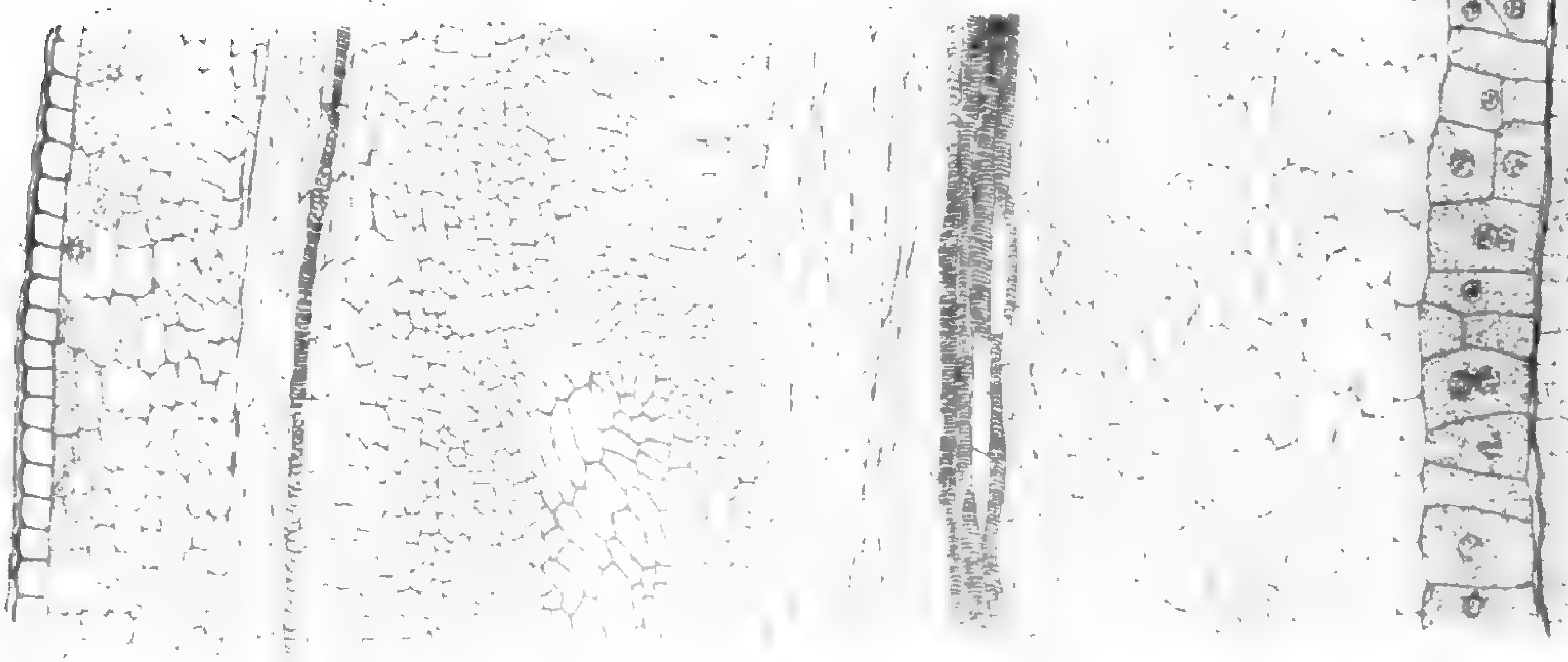

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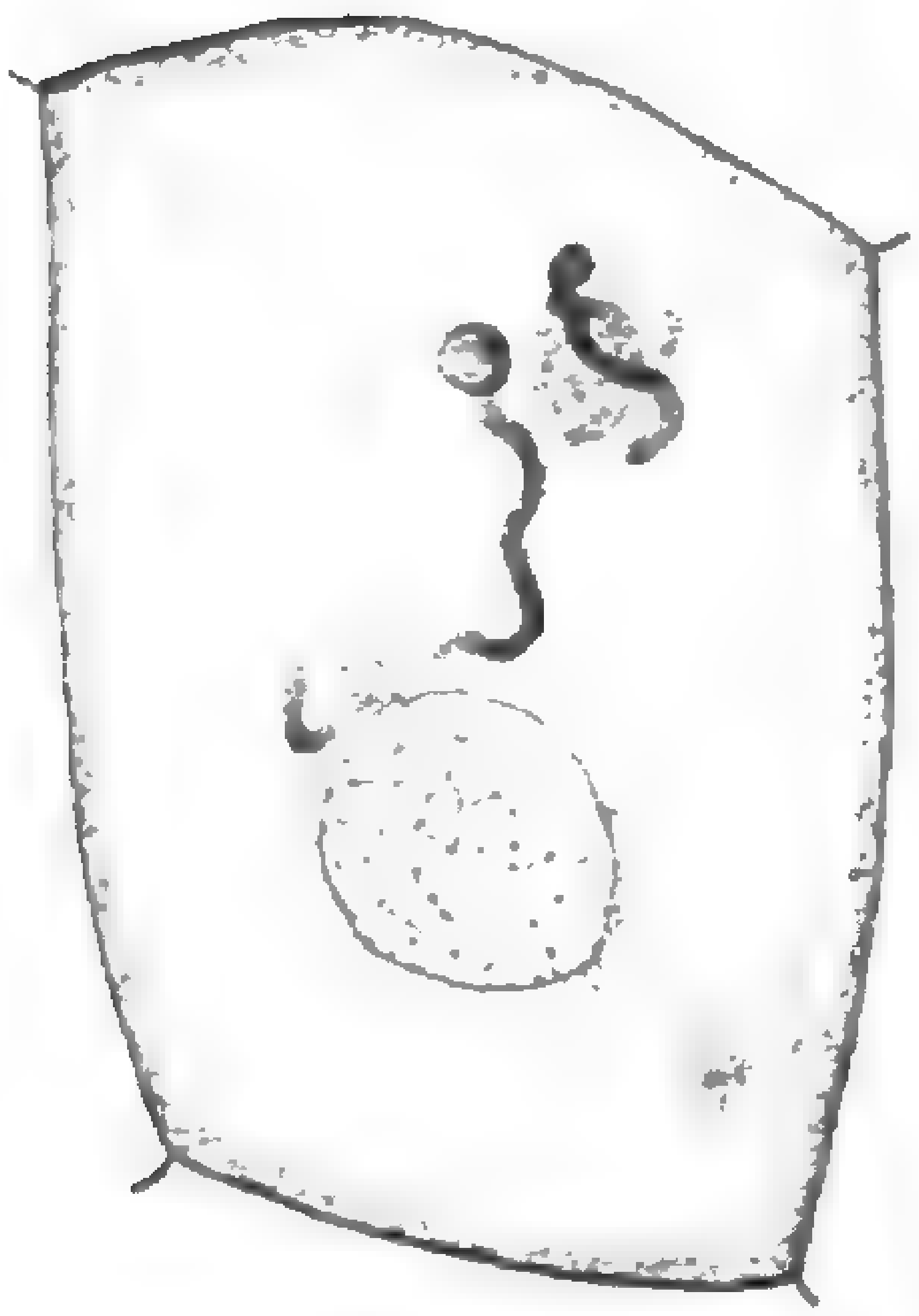

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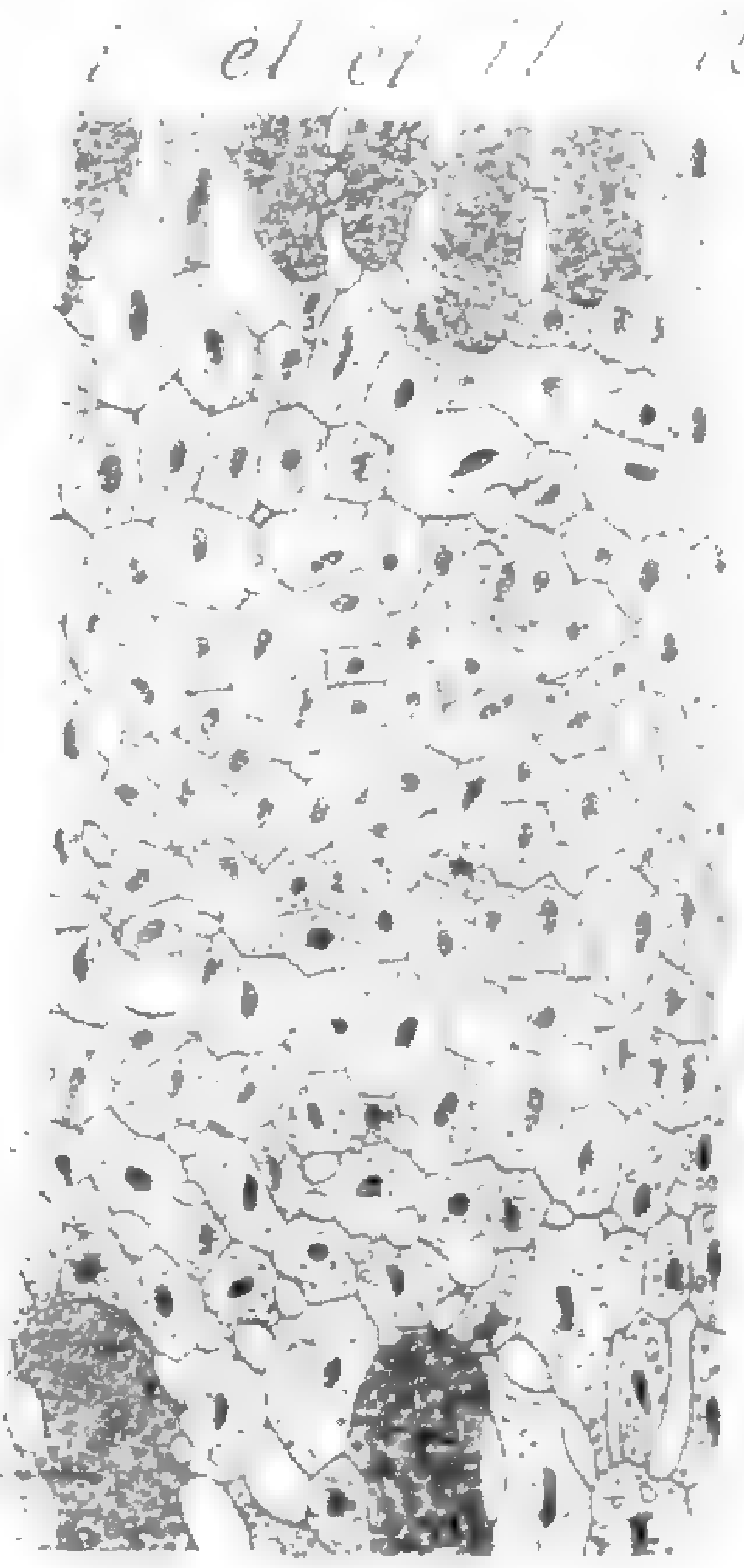

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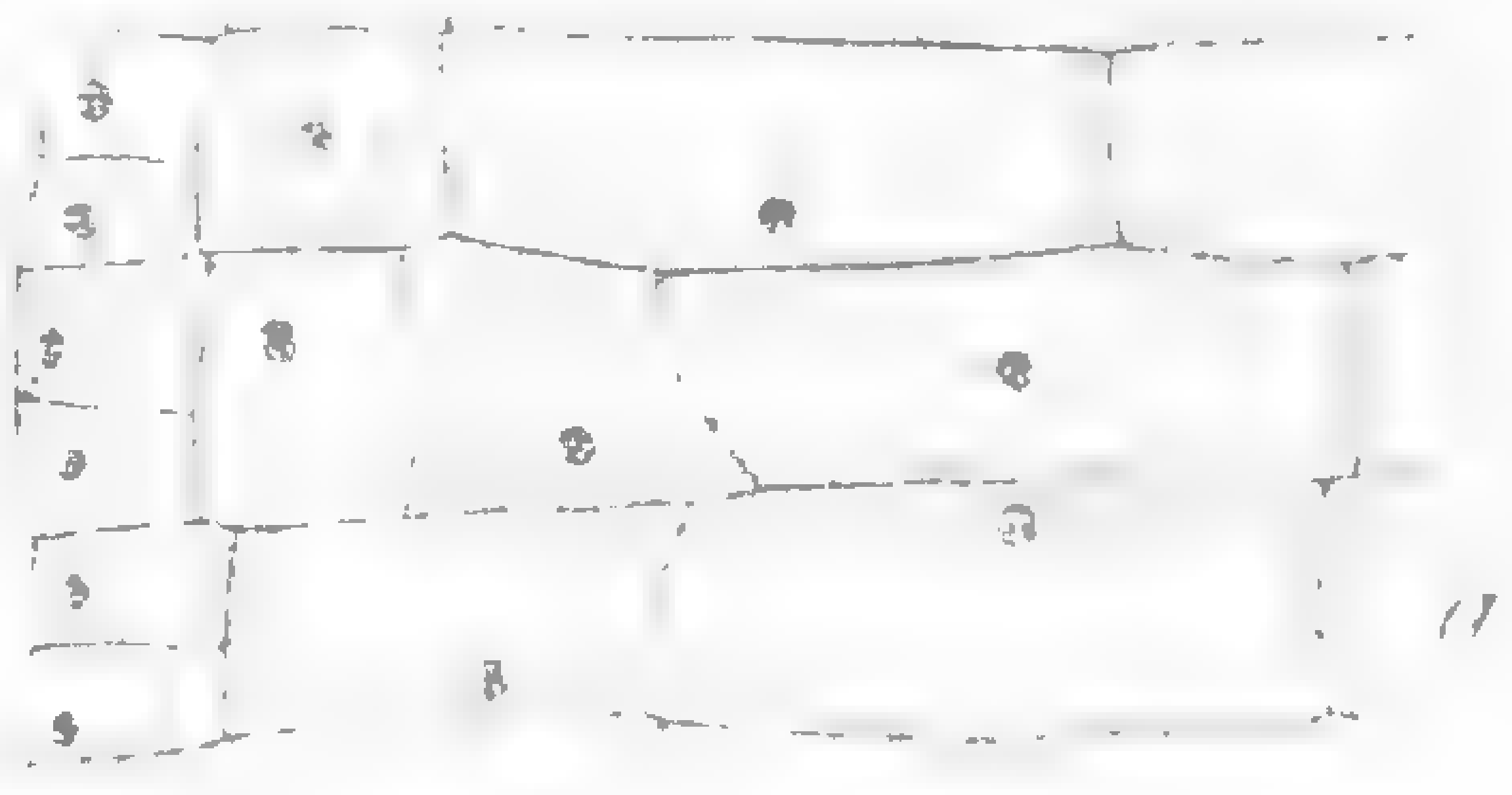

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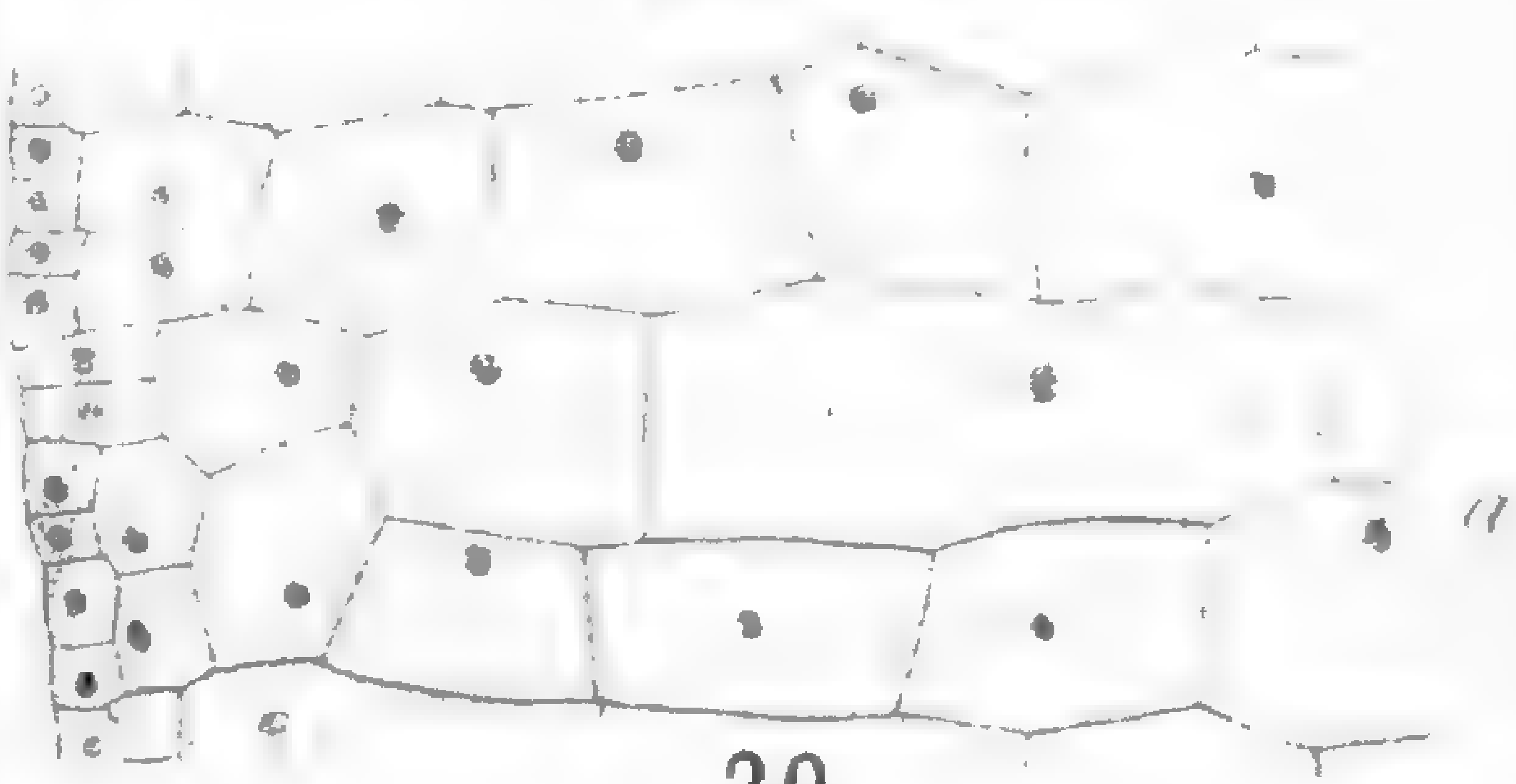

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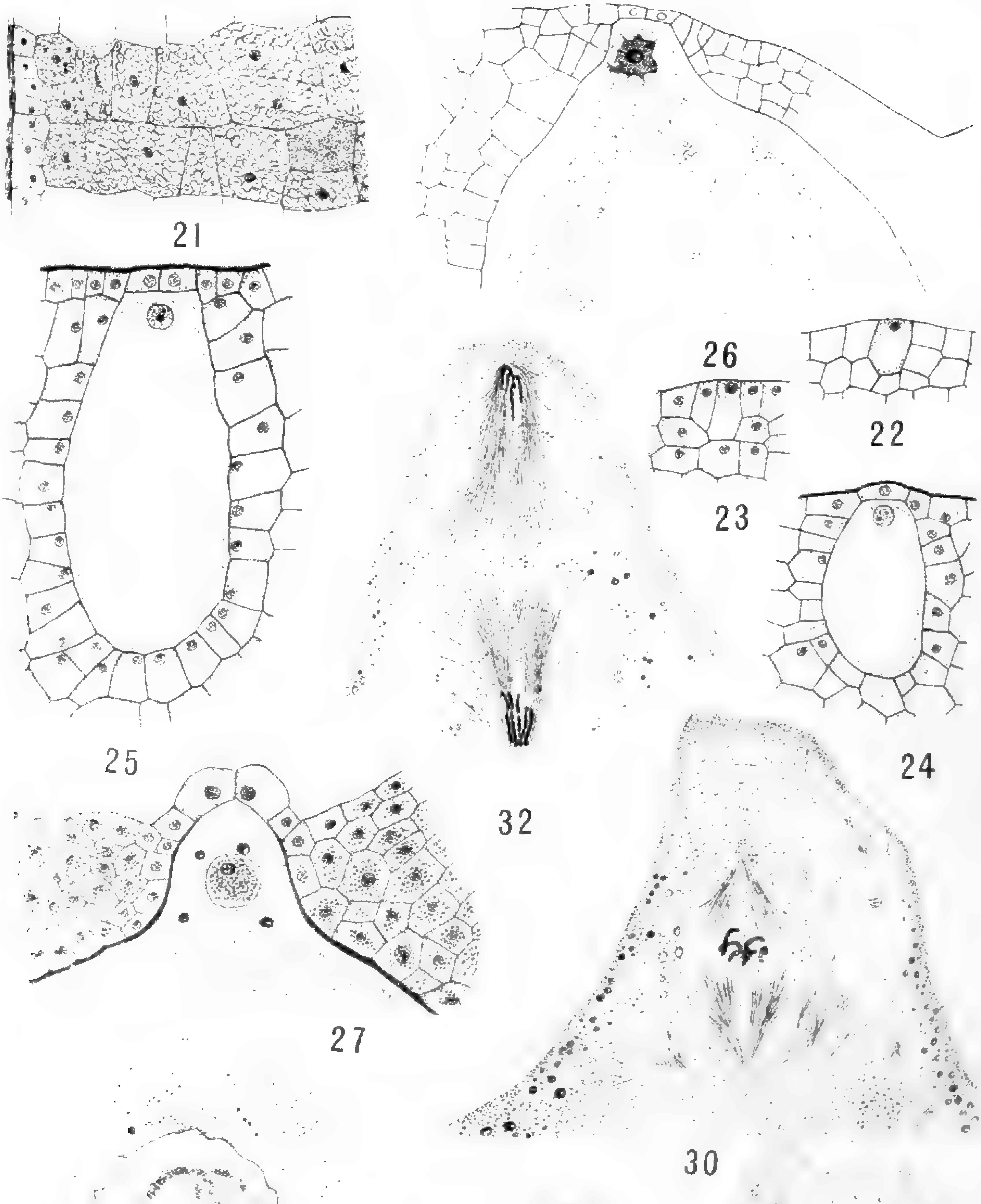
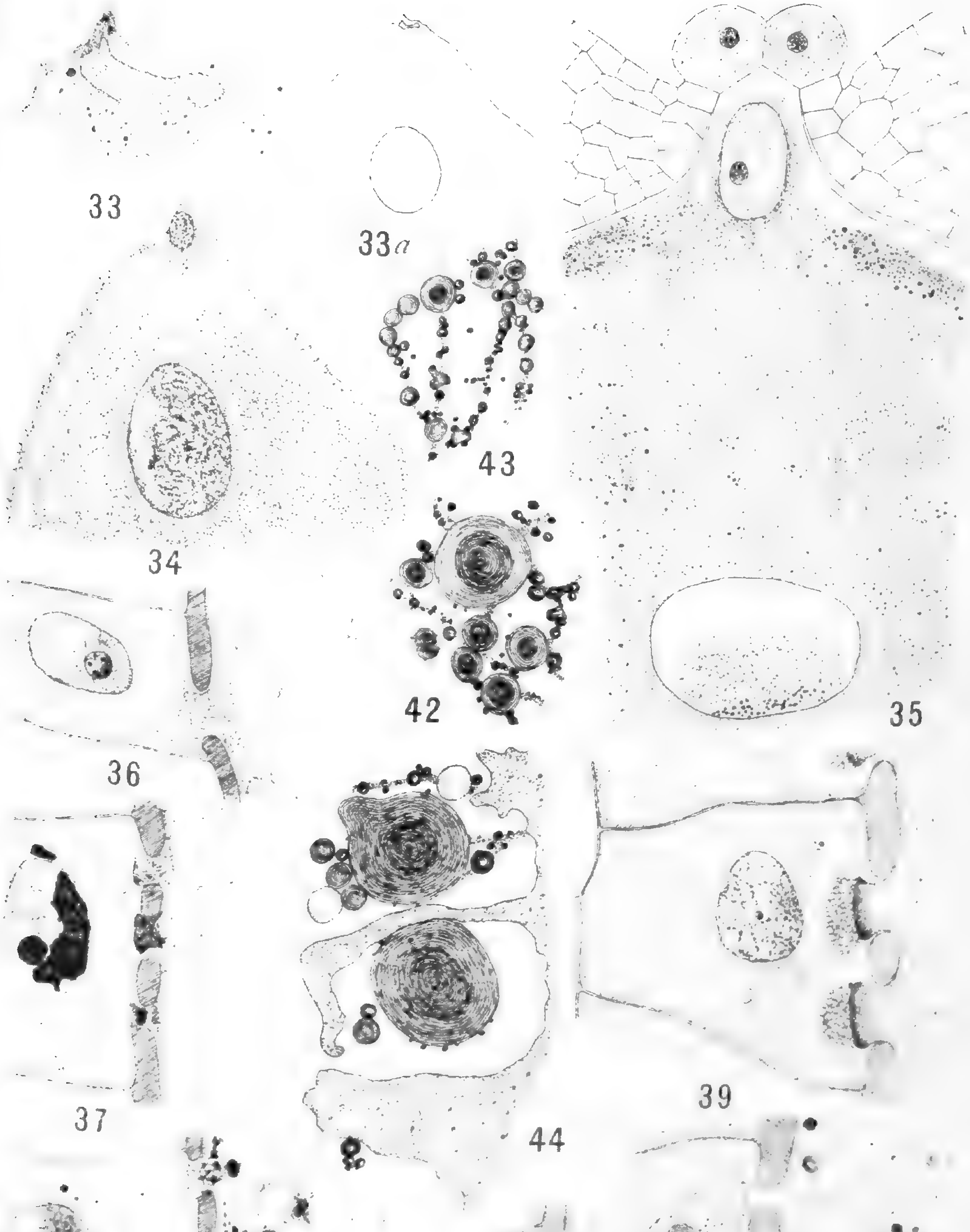
CHAMBERLAIN on DIOON



CHAMBERLAIN on DIOON



CHAMBERLAIN on DIOON

FIG. 11. Longitudinal section through integument and adnate portion of nucellus: *e*, epidermis; *el*, longitudinally elongated cells of stony layer; *et*, transversely elongated cells of stony layer; *ej*, endosperm jacket; *g*, endosperm; *i*, isodiametric cells of stony layer; *ib*, bundle of inner vascular system; *if*, inner fleshy layer of integument; *il*, inner layer of longitudinally elongated cells of stony layer; *n*, adnate portion of nucellus; *ob*, bundle of outer vascular system; *of*, outer fleshy layer of integument; *p*, parenchyma cells of outer fleshy layer; *s*, stony layer; *t*, cells containing tannin. ×2.

FIG. 12. Section showing endosperm (*e*), megaspore membrane (*m*), and endosperm jacket (*ej*). ×350.

FIG. 13. Cell of endosperm jacket showing one normal nucleus and a free spirem of another nucleus. ×350.

FIG. 14. Longitudinal section through abscission layer; *t*, cells containing tannin. ×112.

FIG. 15. Section of archegonia early in December, showing endosperm somewhat raised over the archegonia. Natural size.

FIG. 16. Section of archegonia showing beginning of archegonial chamber. Natural size.

FIG. 17. Section of archegonia just after formation of ventral canal nucleus. ×5.

FIG. 17*a*. The same, natural size.

FIG. 18. Transverse section of megaspore membrane. ×900.

FIG. 19. Section of lateral endosperm at a period when archegonium initials are forming at the apex; 280 cells in entire periphery of section. ×88.

FIG. 20. Similar section at a later stage, 780 cells in periphery; the two rows of cells marked *a* correspond to the single row *a* of *fig. 19*. ×88.

FIG. 21. Peripheral portion of endosperm at period of germination. ×88.

FIGS. 22–23. Archegonium initials. ×88.

FIG. 24. Archegonium, Dec. 21. ×88.

FIG. 25. Archegonium early in January. ×88.

FIG. 26. Upper portion of archegonium. ×88.

FIG. 27. Upper portion of archegonium, March 7. ×88.

FIG. 28. Upper portion of archegonium, May 13, over two months after cone was picked. ×88.

FIG. 29. Nucleus of central cell and nucleolus-like bodies in the cytoplasm. ×350.

FIGS. 30–32. Stages in the division of the nucleus of the central cell to form the ventral canal nucleus and egg nucleus. ×350.

FIG. 33. Ventral canal nucleus. ×350.

FIG. 33*a*. Upper portion of egg, showing ventral canal nucleus and egg nucleus. ×22.

FIG. 34. Ventral canal nucleus and egg nucleus, April. ×41.

FIG. 35. Neck, ventral canal nucleus, and egg nucleus. ×41.

FIG. 36. Portion of jacket cell and egg, showing haustorium, March 9. ×800.

FIG. 37. Jacket and haustoria, March. ×800.

FIG. 38. Porton of egg and jacket cell just after a discharge. ×800.

FIG. 39. Jacket cell and egg showing accumulation of globules over the haustoria. ×800.

FIG. 40. Similar haustorium with the globules passing into it. ×800.

FIG. 41. Jacket cells and haustoria when the egg is nearly ready for fertilization. ×800.

FIGS. 42–43. Details of structure of the egg nucleus. ×1300.

FIG. 44. Small portion of the egg nucleus showing the very irregular outline of the nuclear membrane. ×1300.

TEMPERATURE AND TOXIC ACTION.

CHARLES BROOKS.

(WITH THIRTY-THREE CHARTS)

THE purpose of these experiments, the results of which are presented in this paper, was to determine what might be the modifying effect of temperature on the toxic properties of certain chemicals as shown by the effect of these substances on germination and growth in certain fungi. Since chemical processes as well as plant activities are influenced by temperature, it was thought that additional knowledge in regard to the nature of the physiological action of poisons might be obtained by comparing their effects at the optimum temperature for germination and growth of the plant with results secured under otherwise similar conditions, but at temperatures below and above that which is most favorable for the development of the particular plant.

So far as the writer has been able to learn, the problem of toxic action has never been carefully investigated from this standpoint. It is well known that temperature is an important factor in the processes of plant and animal life, and that changes in temperature may often serve as a stimulus to reproduction, germination, and development. It has also been shown that the response of an organism to certain stimuli may vary with the temperature, and some data have been reported which indicate that this is true when the stimulus is of a chemical nature. THIELE (1) found that the maximum temperature for the growth of *Penicillium glaucum* on grape sugar lies at 31° C., on glycerin at 36° C., on salts of formic acid at 35° C. NÄGELI (2) reported that bacteria were killed at 30 or 110° C. according to the character of the nutrient medium, but his conclusions seem to be based upon results obtained from impure cultures. HEIDER (3) found that the toxic action of certain chemicals upon the spores of *Bacillus anthracis* increases with a rise of temperature. PASTEUR (4) found that bacteria were more resistant to heat in alkaline than in acid milk; but COHN (5) and BREFELD (6) observed no such increased resistance in alkaline solutions. RICHET (7) has reported that with various poisons the toxic dose diminishes in amount with the elevation of the temperature of the body. MATHEWS (**8**) found that a small rise in room temperature increased the toxic action of certain salts upon the eggs of the fish *Fundulus heteroclitus*, but no data in regard to the extent of the injury were reported.

Considerable work has been done in recent years on the effect of toxic agents upon the germination and development of fungi. CLARK (**9**) determined the concentration of various chemical solutions necessary to produce injury, inhibition, and death in certain fungi. He found that a solution of $n/4$ HNO_3 killed the spores of *Sterigmatocystis nigra* within forty-eight hours, that $n/8$ to $n/16$ solutions of the same acid produced total inhibition of the spores, and that $n/32$ gave great injury to the fungus. *Botrytis vulgaris* spores were killed by $n/16$, and the plant was greatly injured by $n/32$ HNO_3. With *Penicillium glaucum*, $n/4$ HNO_3 killed the spores, $n/8$ and $n/16$ totally inhibited germination, and $n/32$ gave decided injury. H_2SO_4 gave similar results, but a concentration of $n/2$ was required to kill the spores of Sterigmatocystis and Penicillium. With $CuSO_4$, $n/4$ killed the spores of Sterigmatocystis, $n/8$ to $n/16$ gave total inhibition, and $n/32$ to $n/64$ caused decided injury. Botrytis spores were killed by $n/16$ $CuSO_4$, inhibited by $n/32$, and the plant greatly injured by $n/64$. The spores of Penicillium were killed by $2n$ and inhibited by n to $n/64$, while decided injury resulted from $n/128$. DUGGAR (**10**) has reported upon special factors that influence the germination of fungous spores, and Miss FERGUSON (**11**) has given some of the conditions for germination in various basidiomycetous fungi. These recent papers have only an indirect bearing upon the work that follows, but have been very useful in the suggestion of methods for the solution of the problem.

METHODS.

The effect of the various toxic solutions at the different temperatures was observed by means of the ordinary Van Tieghem cells. The manner of constructing and the method of using these have been fully described by CLARK (**9**) and DUGGAR (**10**).

These cells were never used a second time without being taken apart and thoroughly cleaned. In cleaning, the cells were boiled for twenty or thirty minutes, first in an alkali, then in an acid, and finally in distilled water. They were dried from alcohol and made up in the usual manner. The covers were treated as the cells, except that in each instance they were heated for a longer time, and that they were given one or two final boilings in redistilled water. All flasks, vials, etc., used in these experiments were cleaned with alkali, acid, and distilled water by boiling, as described for the cells.

As a culture medium several vegetable decoctions were tried. It was found that the five fungi used in these experiments grew well upon decoctions made from onions, beets, tomatoes, grapes, parsnips, beans, mushrooms, and sugar beets. Several series of experiments were made with tomato decoction as a medium, but it was found that a sugar beet solution gave less precipitate in the presence of $CuSO_4$ and was in general more satisfactory for the work. In all the experiments reported in this paper beet decoction was used as the nutrient medium. In making the infusion 600 grams of beets were used for every liter of water. At the time of using, the decoction was diluted, by the addition of the toxic solution and water, to one-half of its former nutrient value.

The toxic agents used were HNO_3, H_2SO_4, and $CuSO_4+5H_2O$. The chemicals were of the highest quality that could be obtained and the acid solutions were standardized before using. It is a well-known fact that strong concentrations of $CuSO_4$ precipitate proteids. In solutions at ordinary temperatures in which both are present, this precipitation continues for a long time, thus continually changing the nature of the liquid. Therefore, as it was necessary to make experiments at considerable intervals of time, the toxic agent was not added to the beet decoction until the time of its use in cultures. Stock solutions of the chemicals were made in water that had been carefully redistilled from glass in the presence of an oxidizing agent. Normal or one-half normal solutions were made and these stored in flasks provided with closely fitting rubber stoppers. By means of a series of graduated vials, these stock solutions were diluted and mixed with the beet decoction at the time of using.

The fungi used were *Botrytis vulgaris*, *Monilia fructigena*, *Sterigmatocystis nigra*, *Mucor Mucedo*, and *Penicillium glaucum*. The first two may be and usually are parasitic, and have an optimum temperature that is comparatively low; the last three are saprophytic and grow well at temperatures considerably above the optimum for the first two. It was thought by this selection to obtain more interesting results than with forms more closely related physiologically. Only pure cultures were used. In the test tube cultures from which the spores were obtained for use, the fungi were grown upon cylinders of potato or beet. In either case the liquid in the tubes was a decoction of sugar beets. Other nutrient substances were tried for the test tube cultures, but these usually produced modifications in the growth of the fungi and it was not found advisable to use spores produced on different media in the course of a series of experiments, the results of which were to be compared. The spores used were always taken from cultures that were twelve to sixteen days old. The desired temperatures were secured by means of incubators and a refrigerator.

CLARK has pointed out certain sources of error for Van Tieghem cell cultures exposed to ordinary temperatures; but the placing of cells, made up under ordinary laboratory conditions, at temperatures ranging from 5° to 30° C., gave additional opportunity for error. The cells were not entirely closed until they had been left for several minutes in the temperature at which they were to remain. This gave opportunity for adjustment of air pressure in the cell, but it did not in all cases prevent the condensation of water vapor upon the cover glass. The small drops of water thus formed not only increased the evaporating surface but also modified the vapor pressure in the cell. The small water drops adjacent to the hanging ones of the nutrient solution seemed to sometimes unite with them, thus changing both their size and concentration. When the cultures were made in the dry air of a furnace heated room no difficulty was experienced, but cells made upon sultry days, or when the air of the culture room was humid from any cause, gave a visible condensation when placed at low temperatures. Even with the greatest precaution this difficulty was not entirely overcome.

It was found difficult to examine the cultures placed at various temperatures without interfering with the structure and condition of the cells. Examinations were made at temperatures as near as possible to those at which the fungi were growing, and results obtained from damaged cells were rejected. All cultures were observed every twenty-four hours and notes taken of percentage of germination, length of germ tube, fruiting, and any peculiarities in germination or development. More frequent observations would have been of interest, but they were not made on account of the increased source of error that would have been thus introduced. Any sources of error that were not otherwise provided for were guarded against by always making duplicate cultures. The experiments with the three chemicals were always made at different times, and as control cultures were made in every case, the growth of each fungus in a nutrient medium at a particular temperature was tested six times.

The vitality of spores that had been subjected to the action of an inhibiting toxic agent was tested by transfer to a nutrient non-toxic medium. An attempt was made to accomplish this transfer by removing the drop of the toxic solution with sterilized filter paper and replacing it by a drop of beet decoction. This method left some part of the former solution as well as any precipitate that had been formed adhering to the cover glass, and was therefore adandoned. All transfers that are concerned in the following data were made by means of a sterilized platinum needle. The spores were in every case transferred to a drop of beet decoction on a clean cover glass. The medium used in the bottom of the cells was in this, as well as in all other cases, the same as that of the hanging drop. It is quite evident that the above method of transferring did not prevent a small amount of the toxic solution being carried into the new drop by the spores and the needle, but the results obtained indicated that this small per cent. of the toxic agent either served as a very slight stimulus to germination and growth or exerted no appreciable influence.

Early in the work it was seen that results obtained from the exposure of the fungous spores to the toxic agent must be considered entirely apart from the data secured in cases where the mycelium was acted upon by the toxic solution. Therefore, when a particular toxic solution gave no germination at one temperature, but did at others, the ungerminated spores were in no case transferred; *i. e.*, transfers were made only with those solutions that gave no germination even at the optimum temperature at the end of the given time.

By a series of preliminary experiments strengths of toxic solution and time of exposure were determined, such as would give the greatest contrast in the results obtained at the various temperatures.

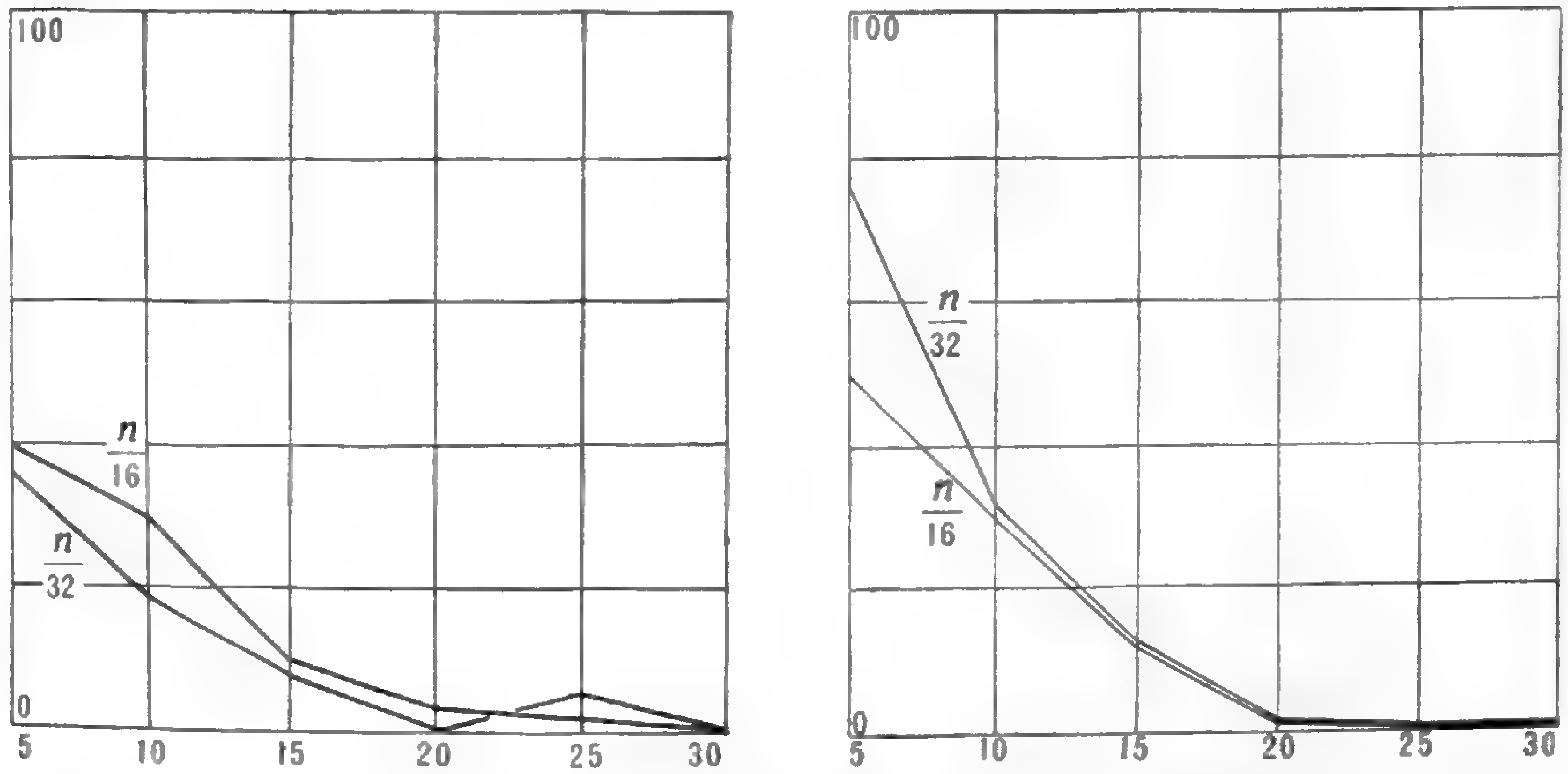
DATA AND DISCUSSION.

In order to put the results obtained in a form as concise as possible, charts 1*a*–12*c* have been prepared, and the greater part of the data obtained is expressed in these by means of curves.

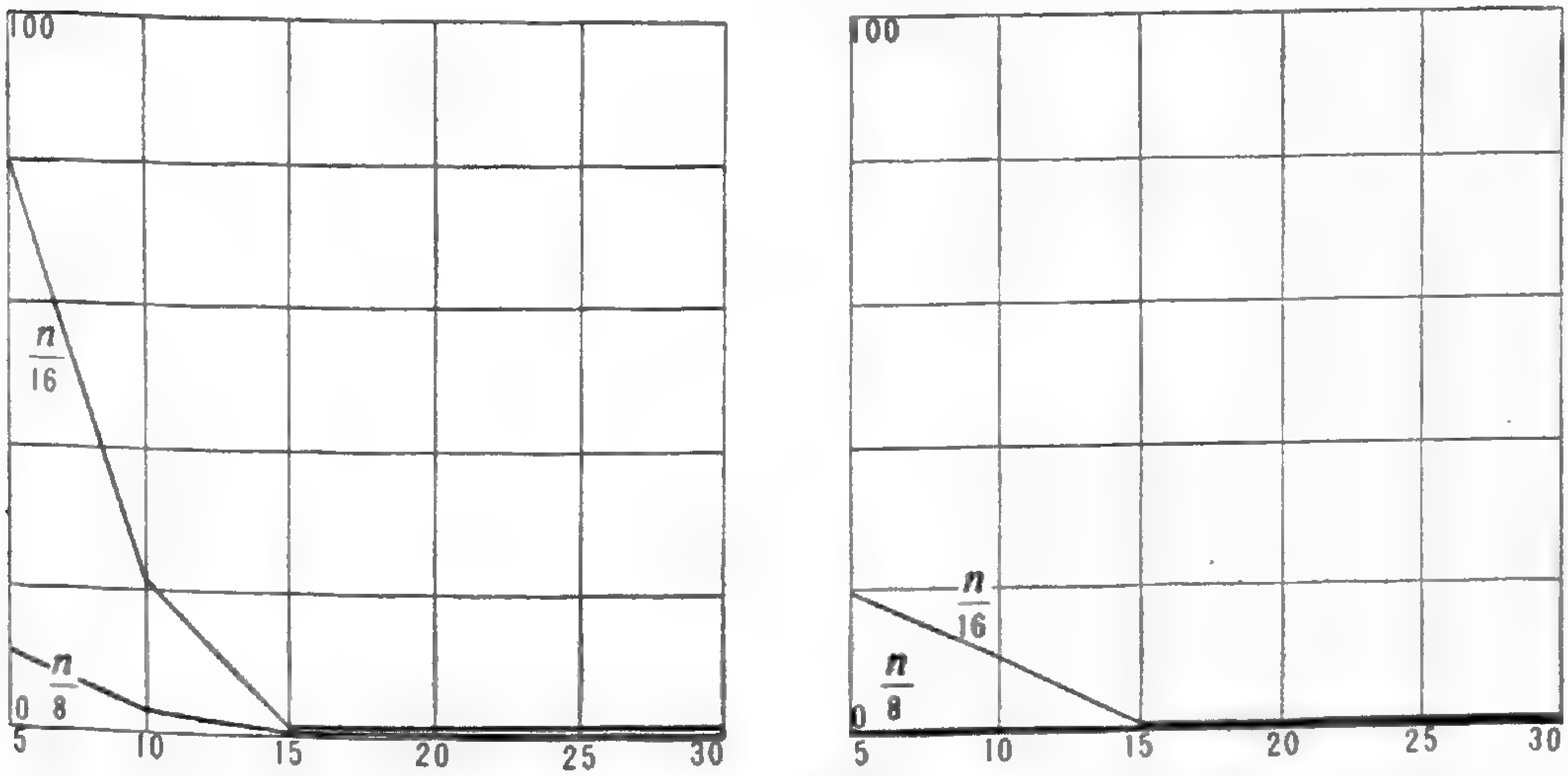
In charts 1*a* to 10*c* inclusive, the abscissae indicate the temperatures at which the fungus was kept in culture, and the ordinates show the per cent. of germination at these temperatures. All the points indicating per cent. of germination at the various temperatures for a particular toxic solution are joined by solid or broken lines; the strength of the toxic solution used is shown by the fraction placed on or near the particular curve. For a further illustration of the meaning of these charts, the curves in chart 2*a* may be considered. These represent the data secured by using $CuSO_4$ with Monilia. With an $n/16$ solution no germination was obtained at 25° and 30°; but at 15°, 12 per cent. of the spores germinated; at 10°, 30 per cent.; and at 5°, 49 per cent.

In charts 1*a* to 5*c* inclusive the results were obtained by exposing the spores for twenty-four hours at the various temperatures in the toxic solution indicated and then transferring them as previously described. The charts are based entirely upon the data secured on the first and second days after transferring. The solid lines indicate the total germination at the end of the second day. The broken lines show the per cent. of germination twenty-four hours after transferring. Where the record of germination was the same for the two days only the solid line is used. It will be noticed that only in a very few instances did spores germinate on the second day.

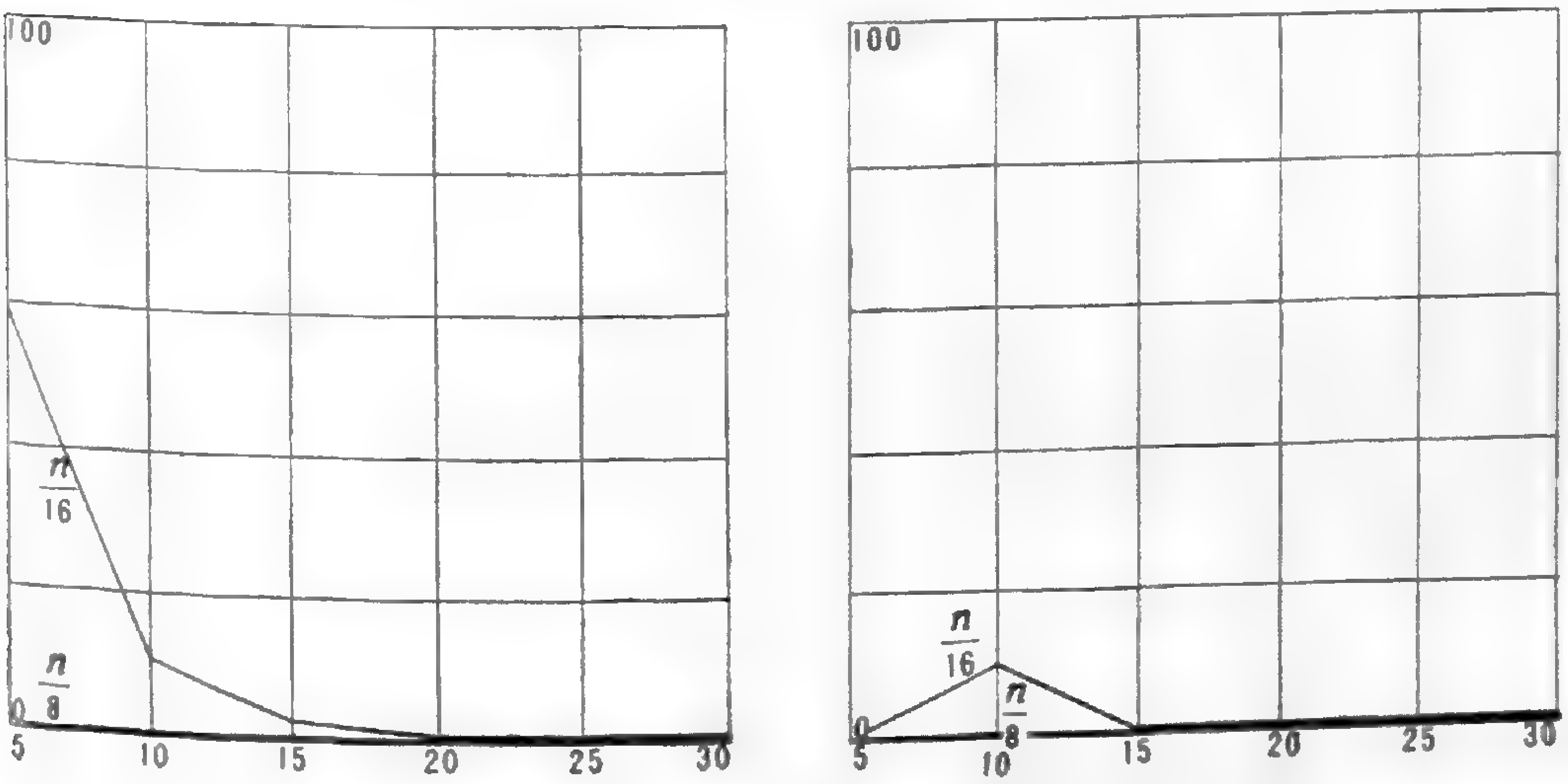
It is readily seen that in most cases the deleterious action of the toxic agents increased very rapidly with the rise in temperature. A comparison of the charts for the various fungi indicates that there are some differences in reactions worthy of special note. Thus, there is a marked drop between 5° and 10° in the germination curves for Botrytis and Monilia, but for no other fungus. With Penicillium the fall comes either between 10° and 15° or between 15° and 20°, while with Mucor and Sterigmatocystis the downward curves begin



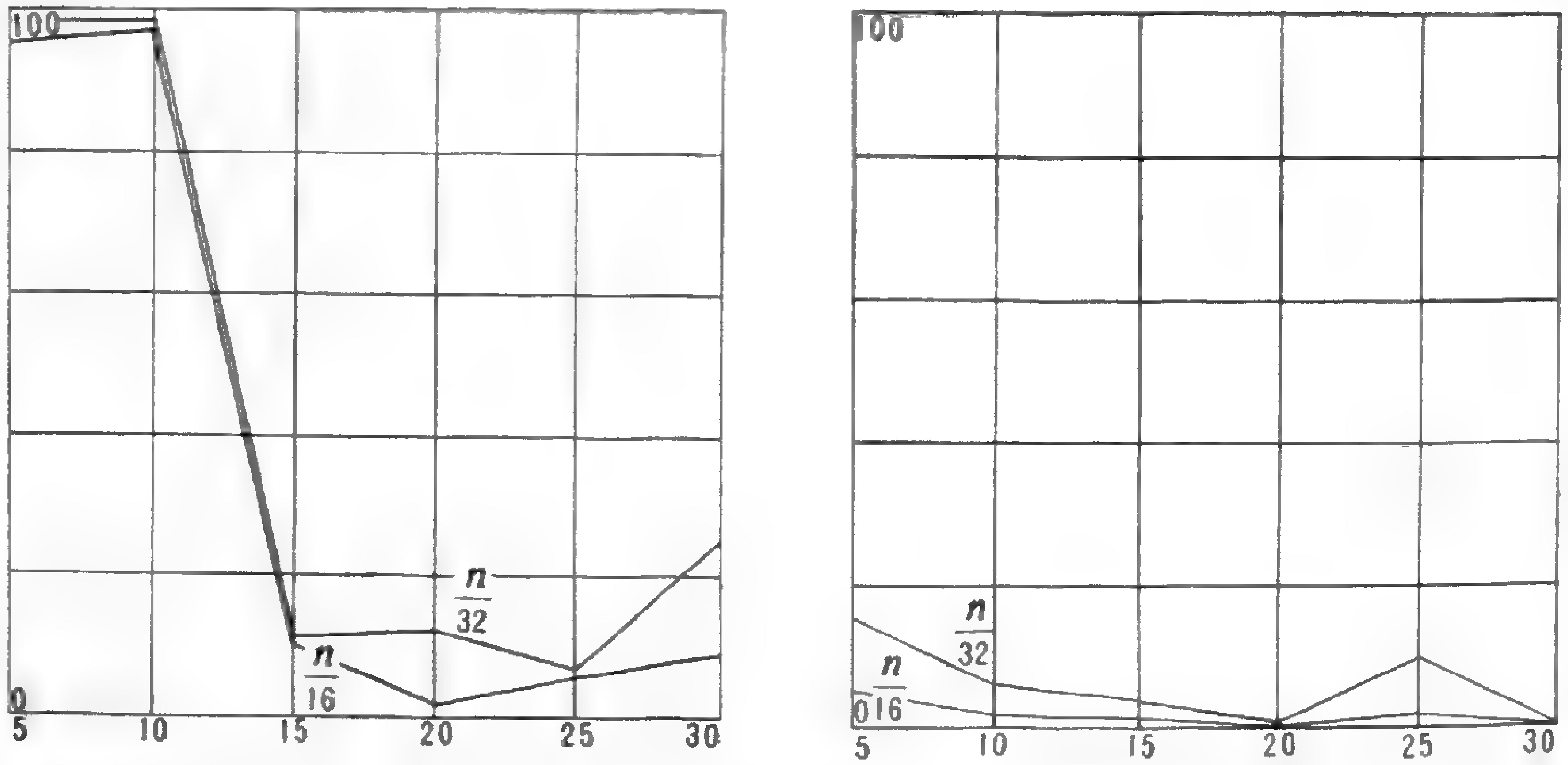
1*a*, Botrytis. **$CuSO_4$.** 2*a*, Monilia.



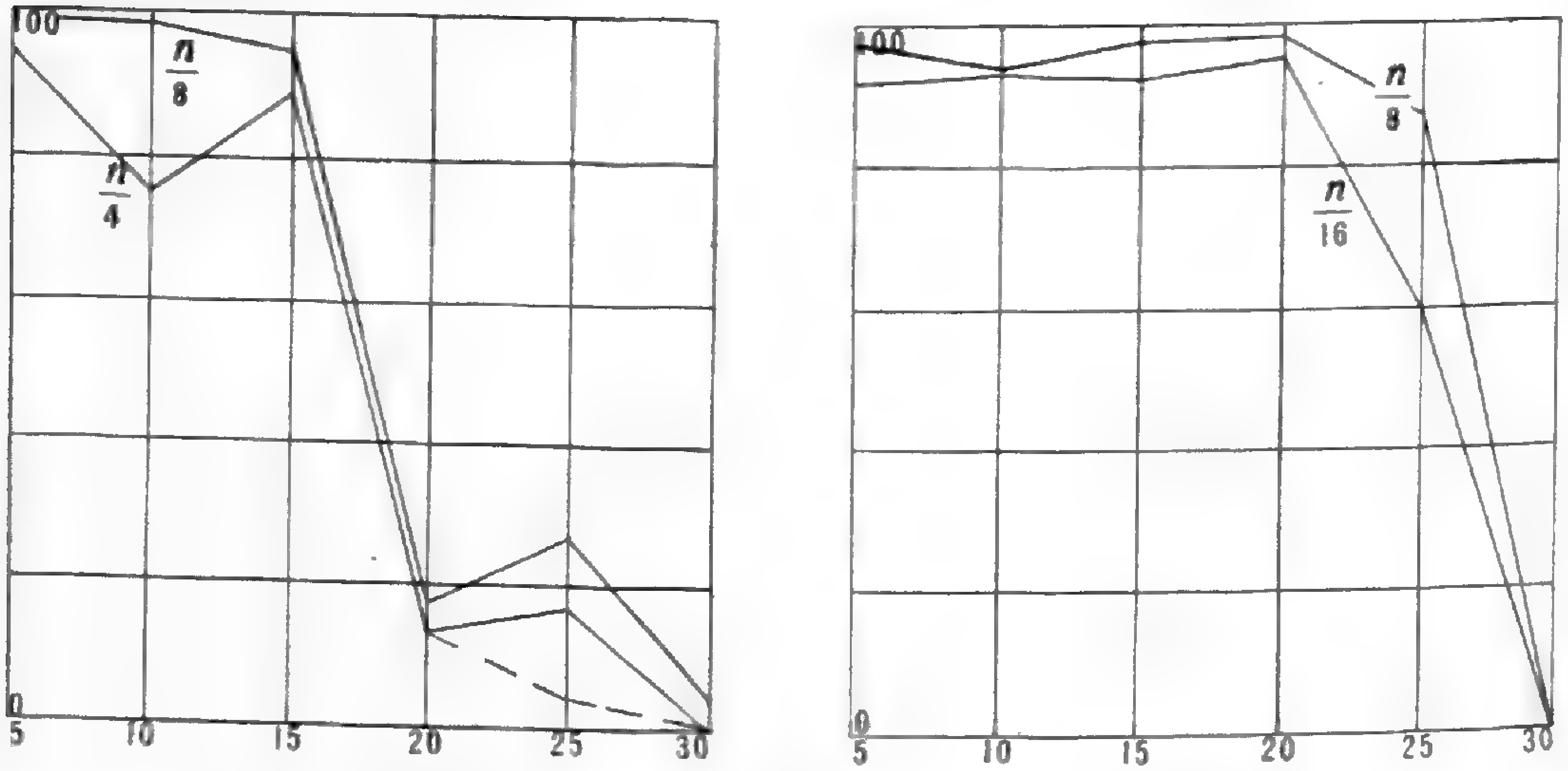
1*b*, Botrytis. **H_2SO_4.** 2*b*, Monilia.



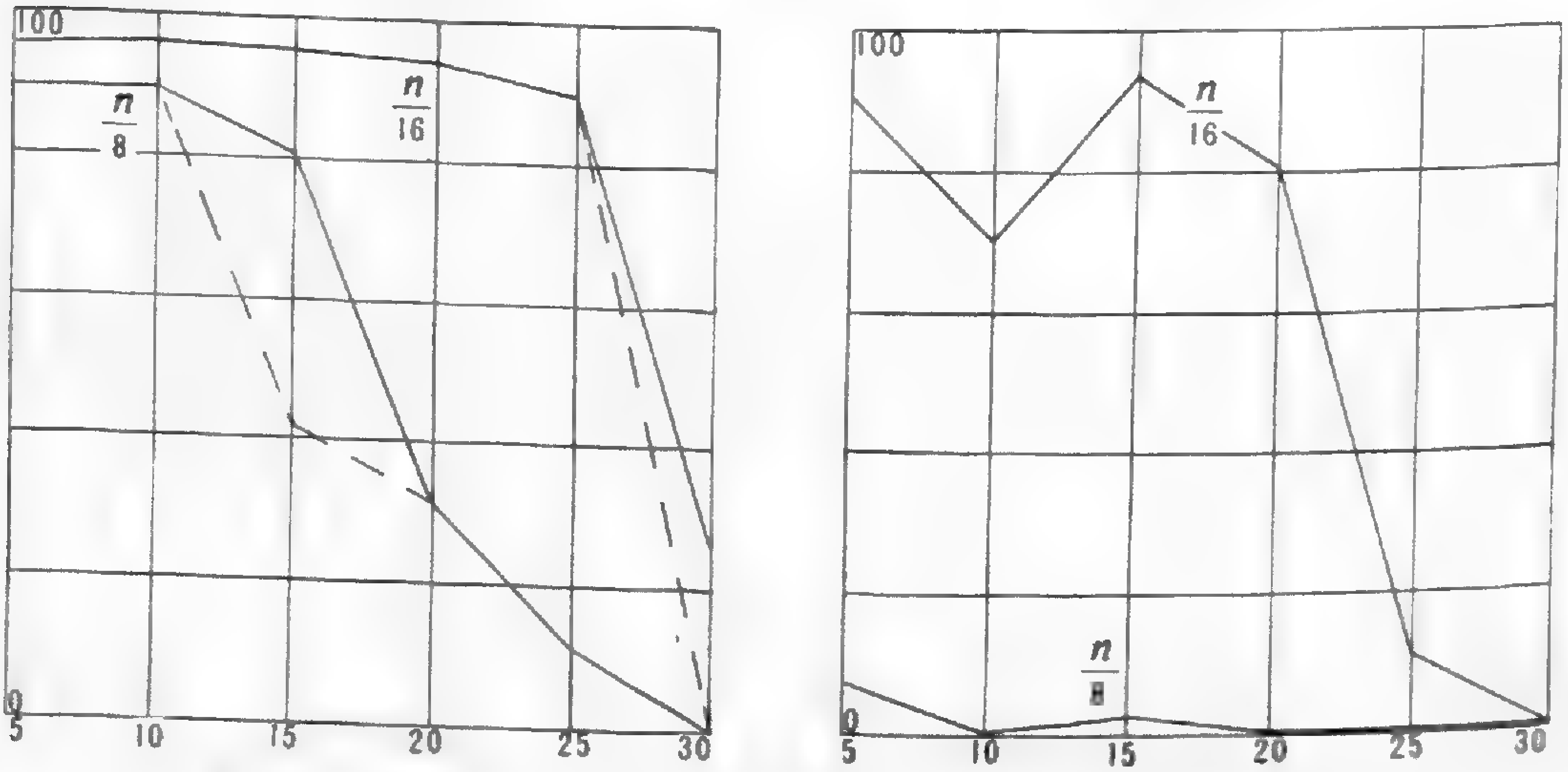
1*c*, Botrytis. **HNO_3.** 2*c*, Monilia.



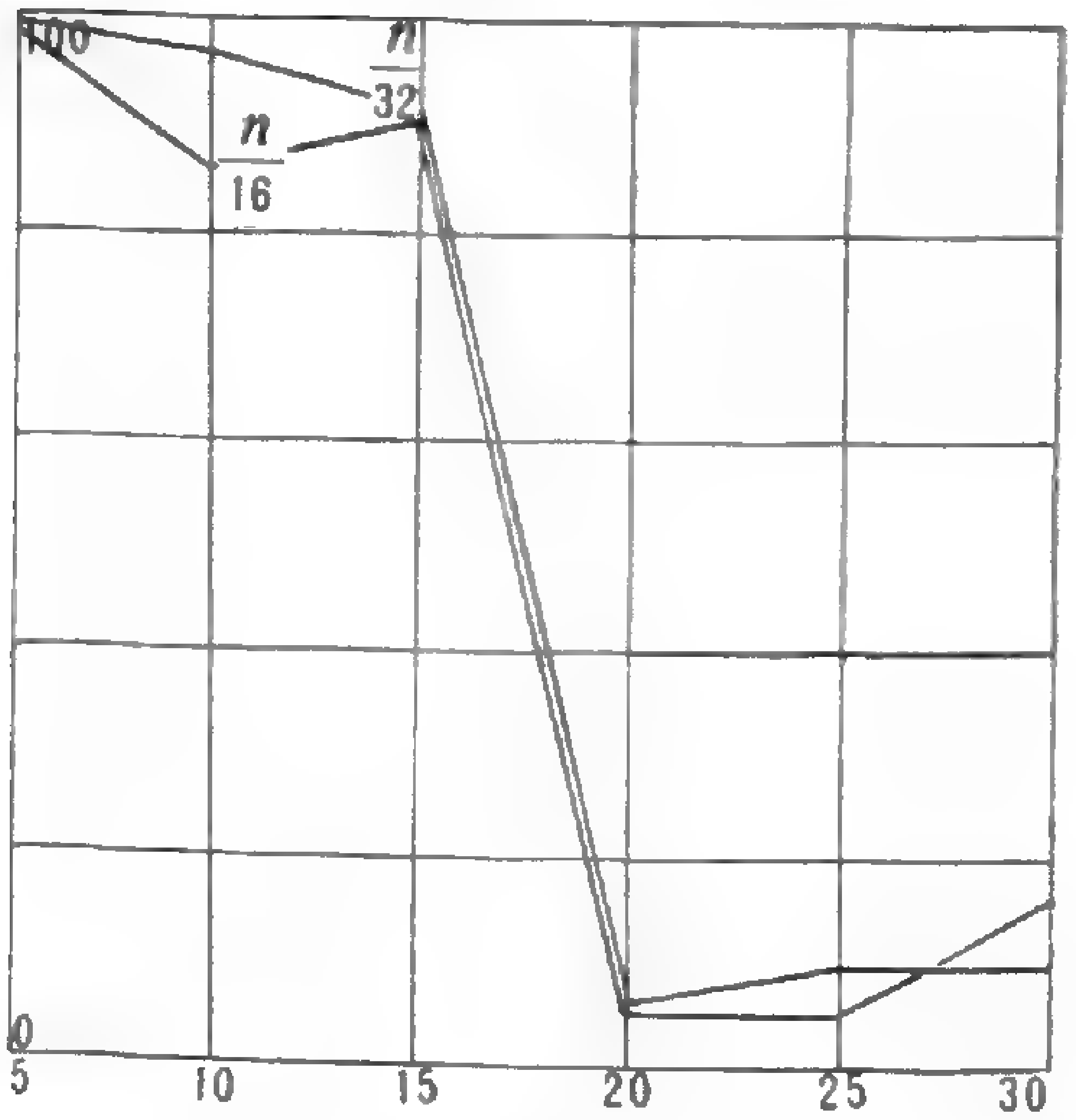
3*a*, Penicillium. **$CuSO_4$.** 4*a*, Mucor.



3*b*, Penicillium. **H_2SO_4.** 4*b*, Mucor.

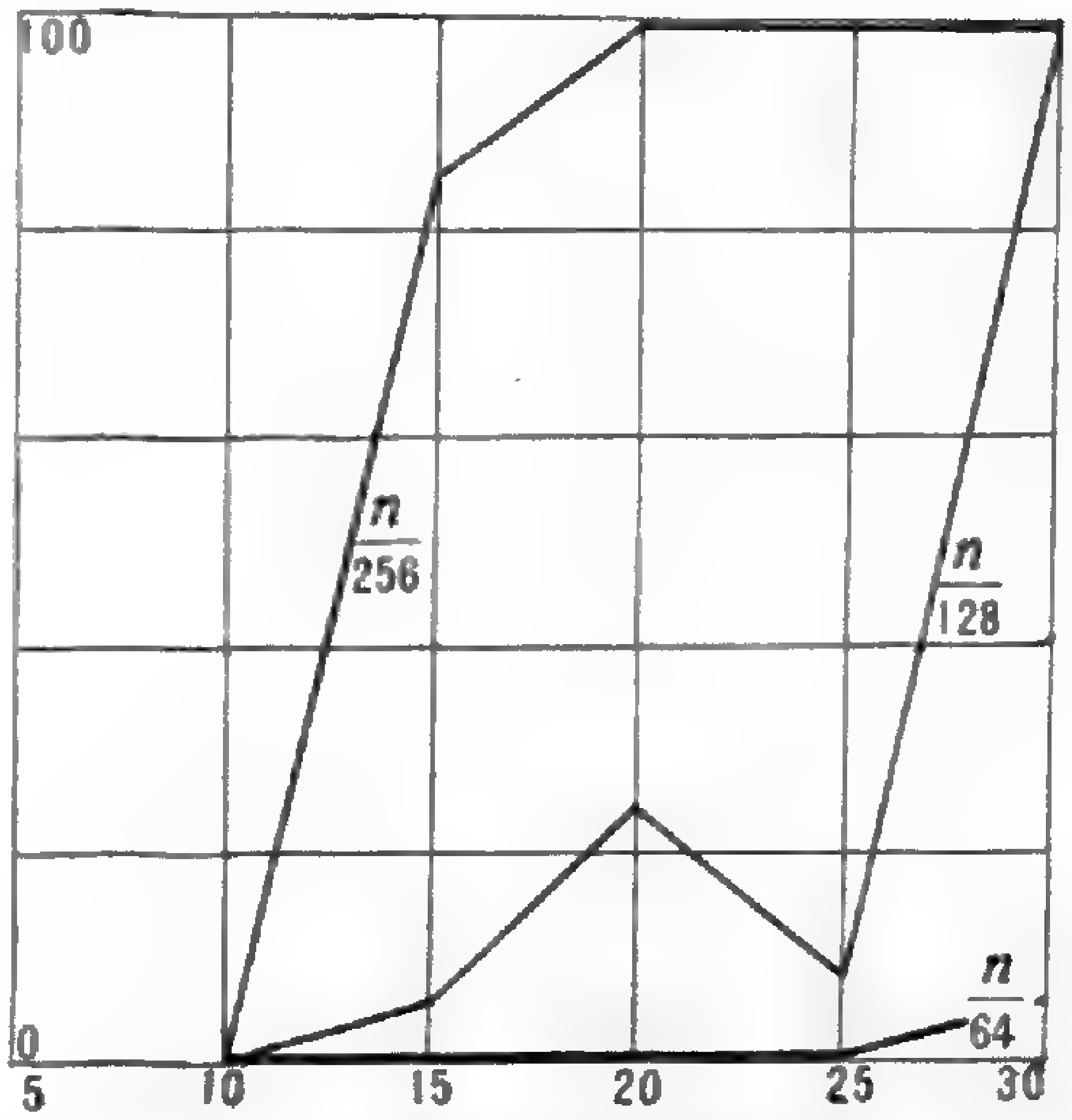


3*c*, Penicillium. **HNO_3.** 4*c*, Mucor.

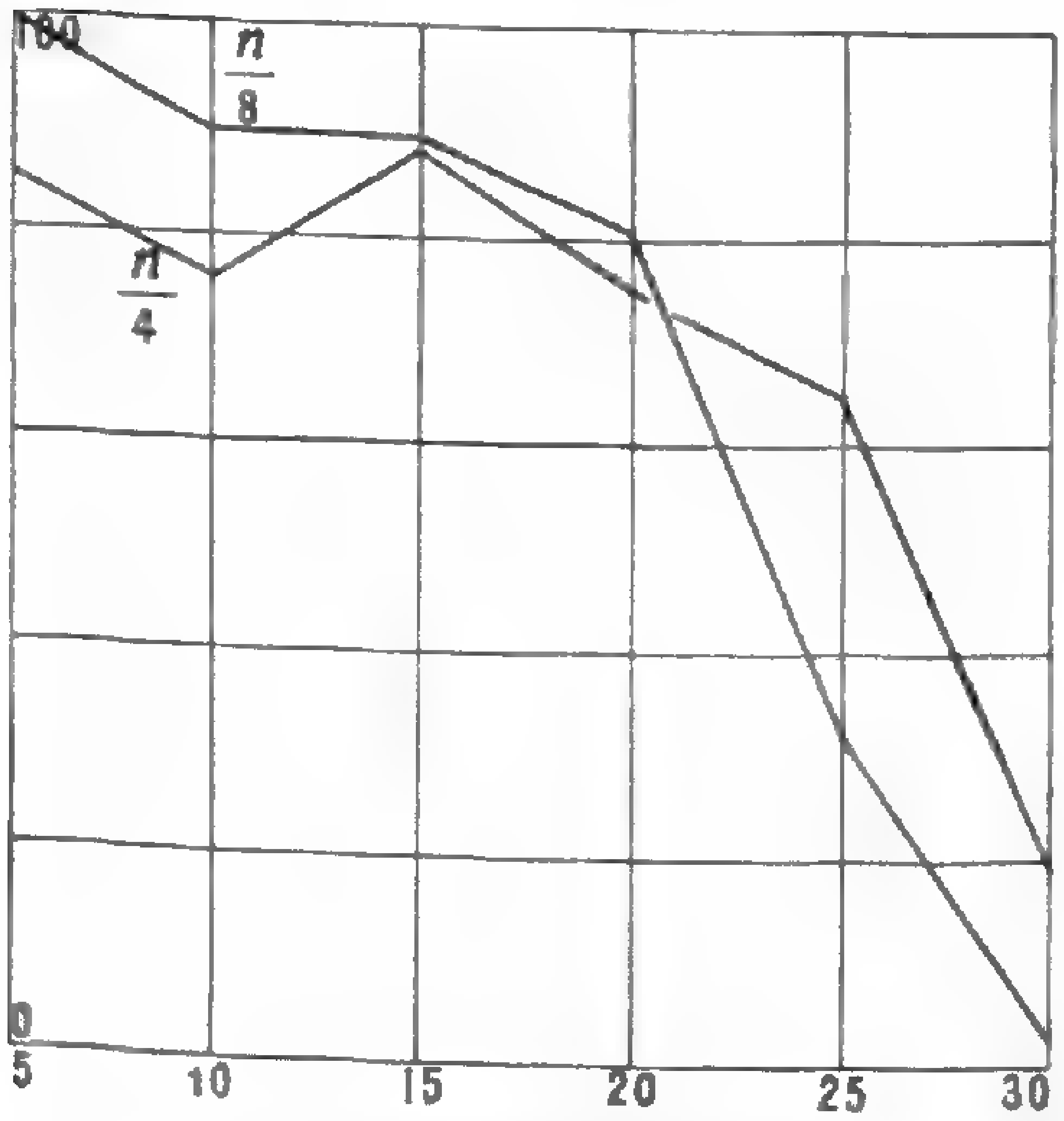


5a, Sterigmatocystis.

$CuSO_4$.

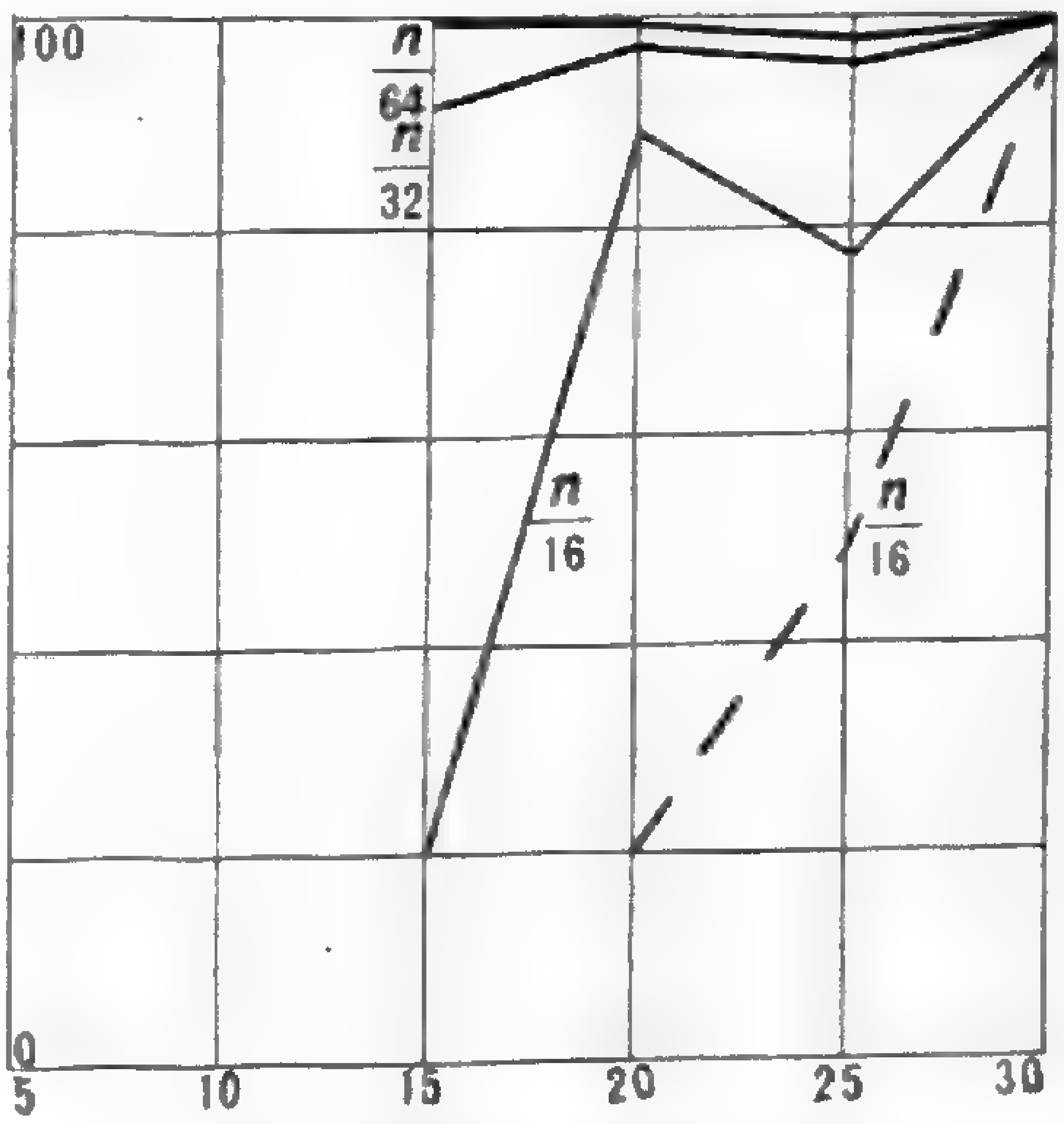


6a, Sterigmatocystis.

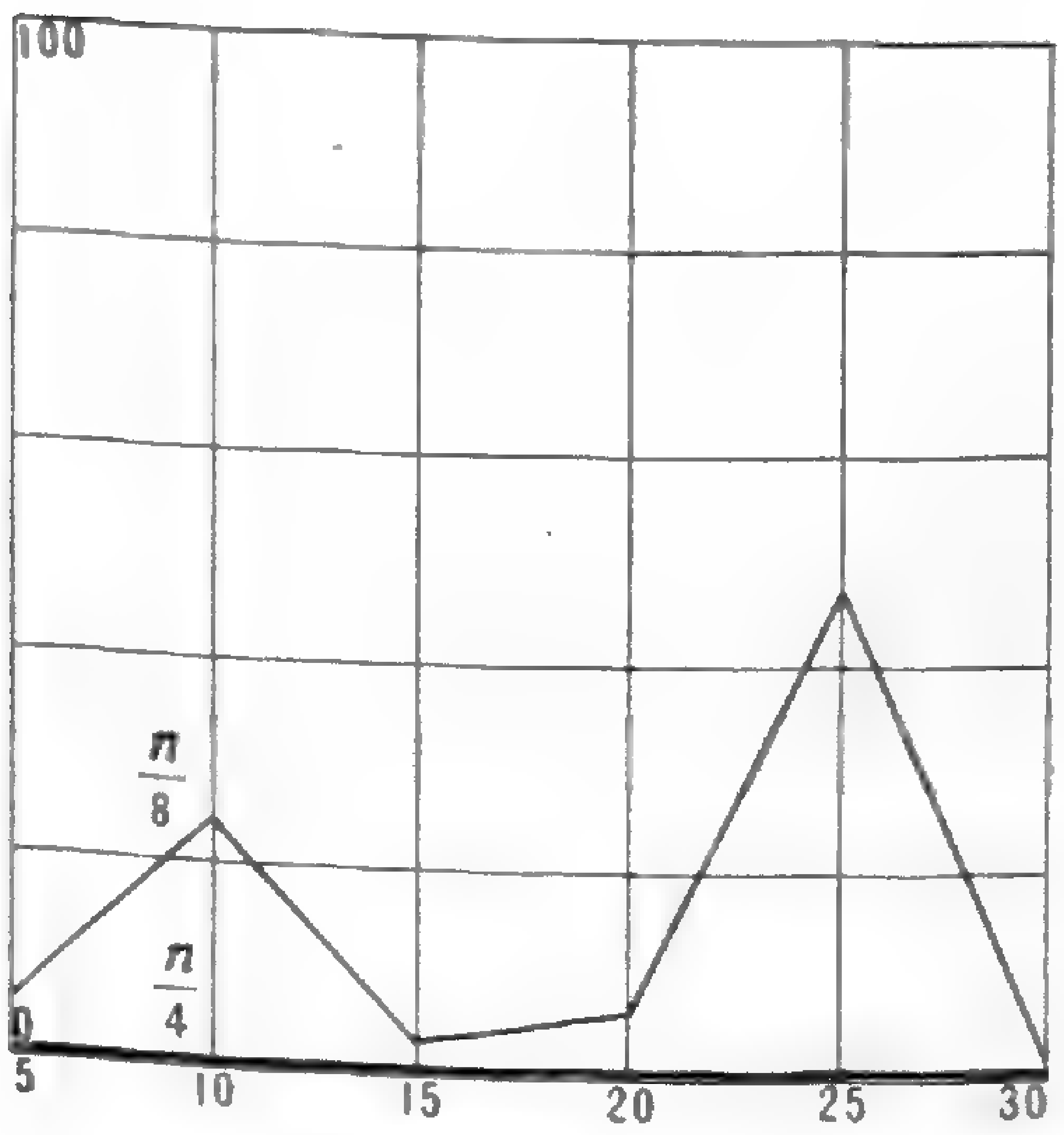


5b, Sterigmatocystis.

H_2SO_4.

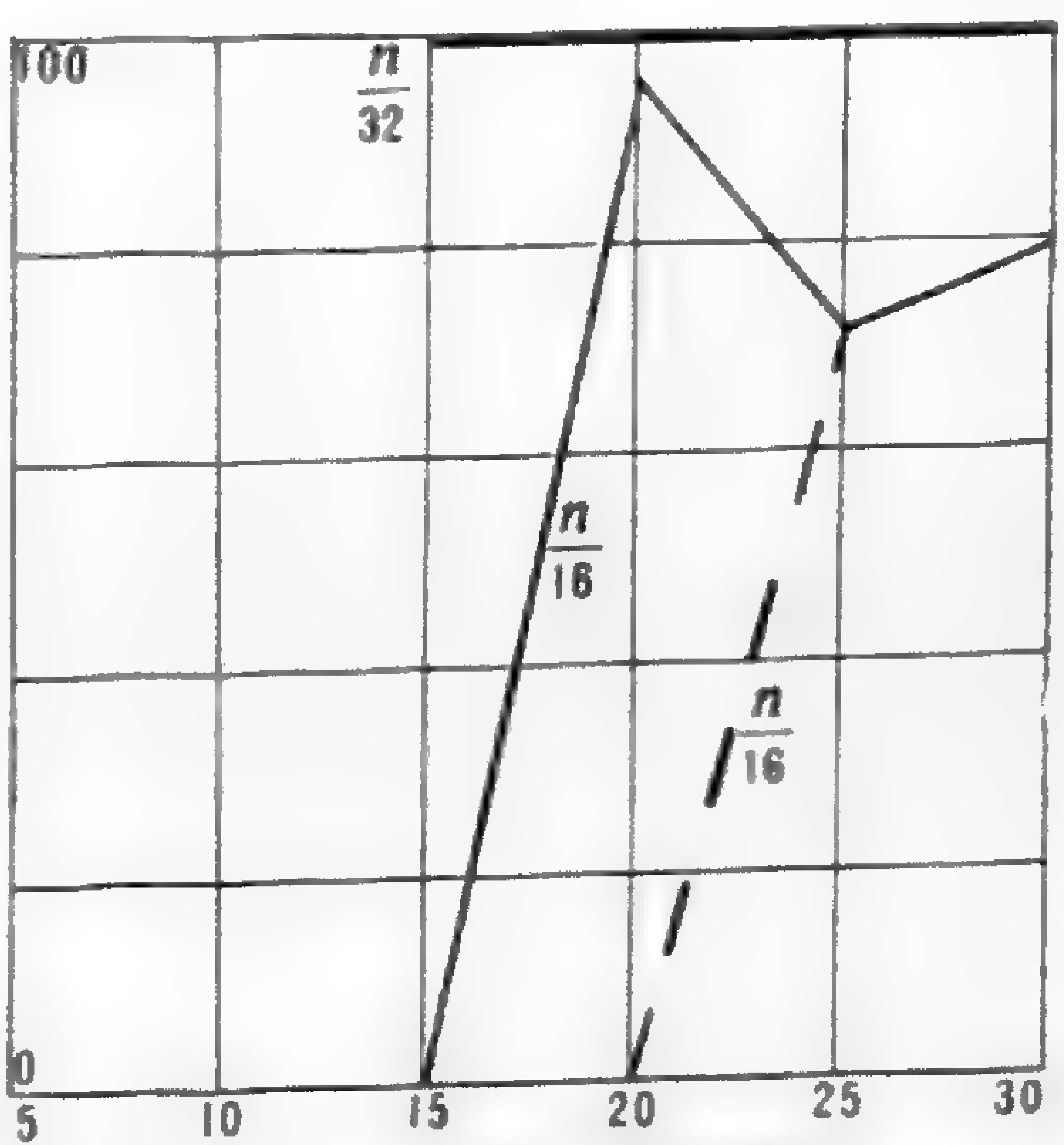


6b, Sterigmatocystis.

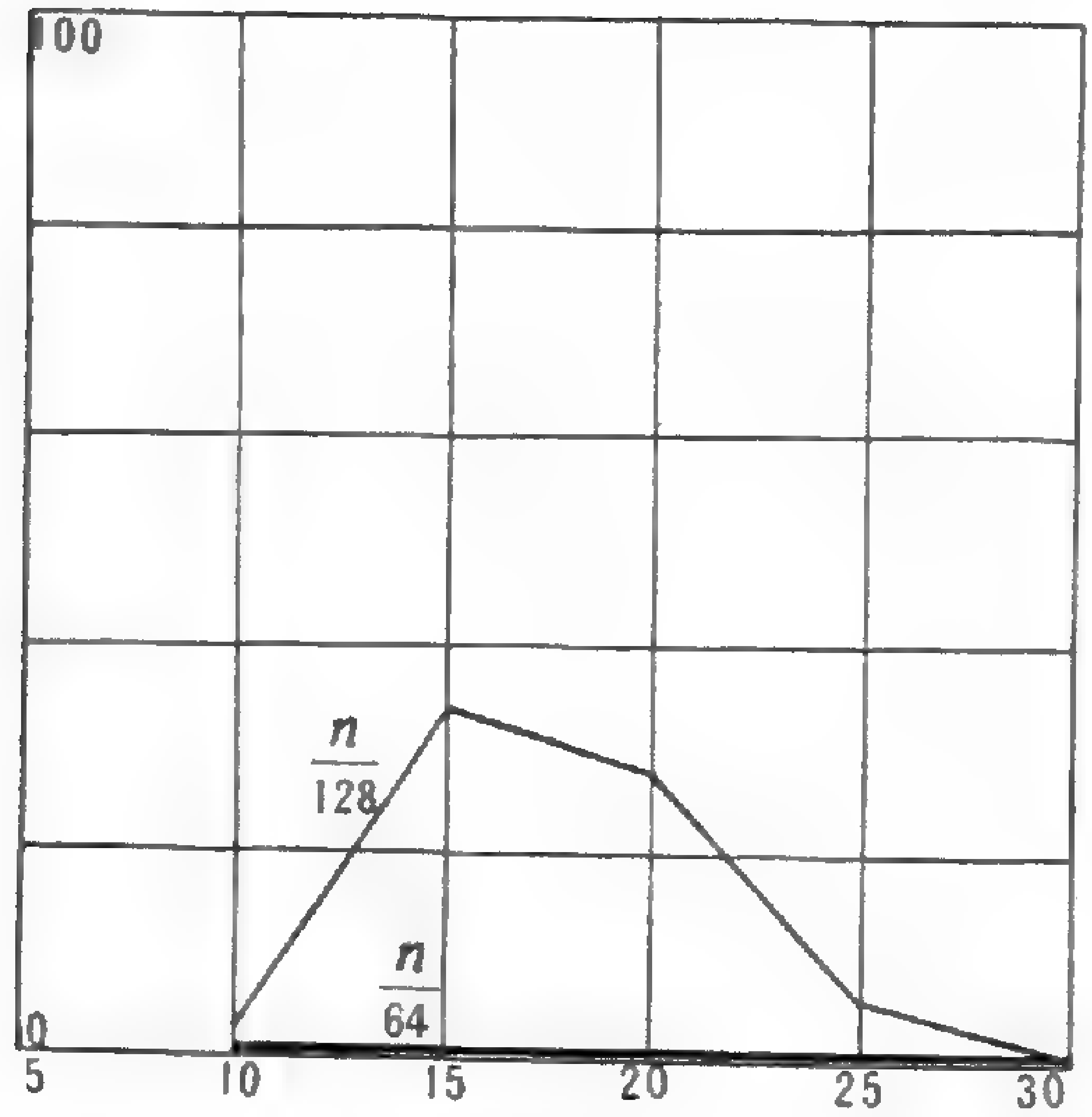


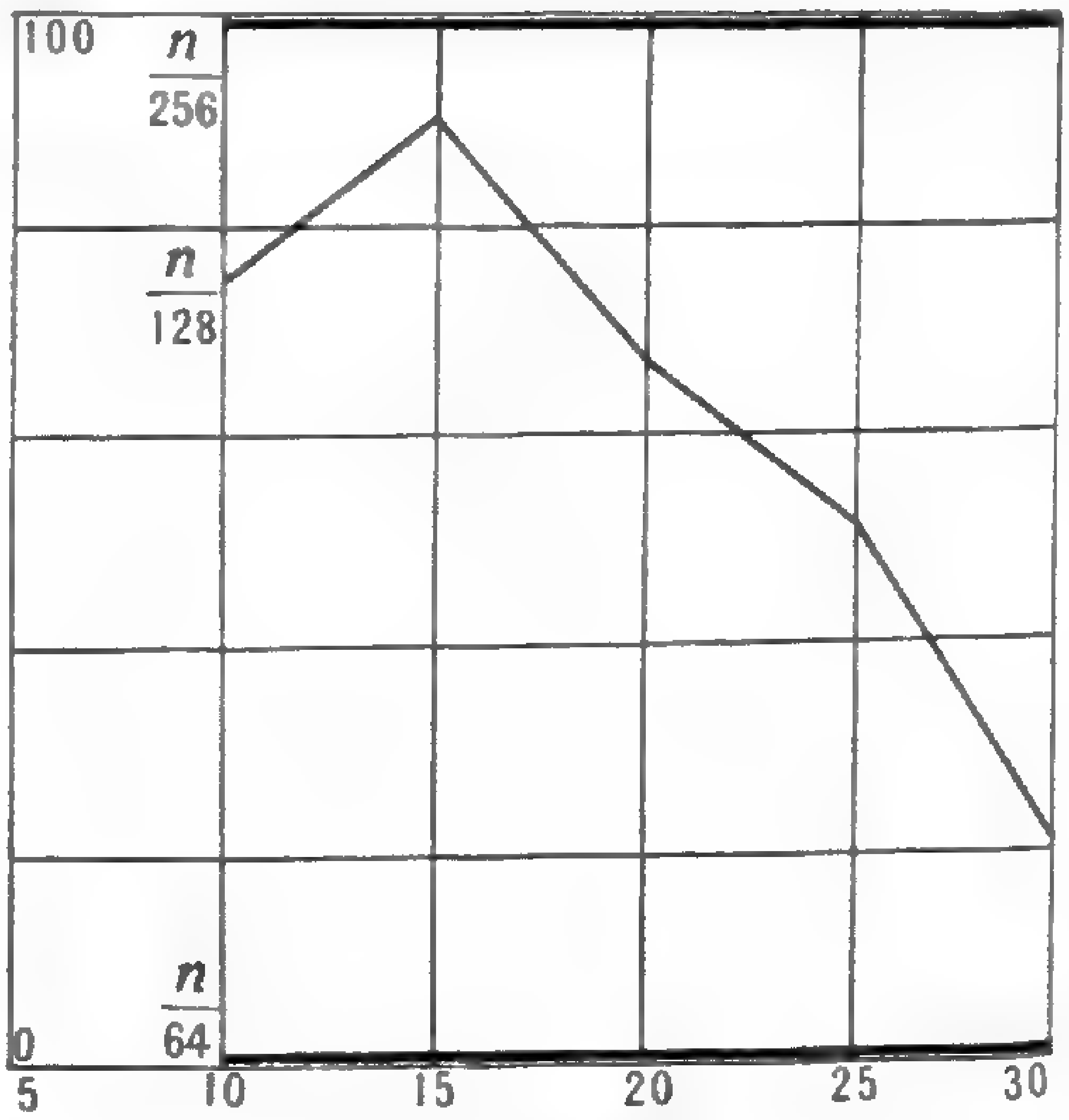
5c, Sterigmatocystis.

HNO_3.

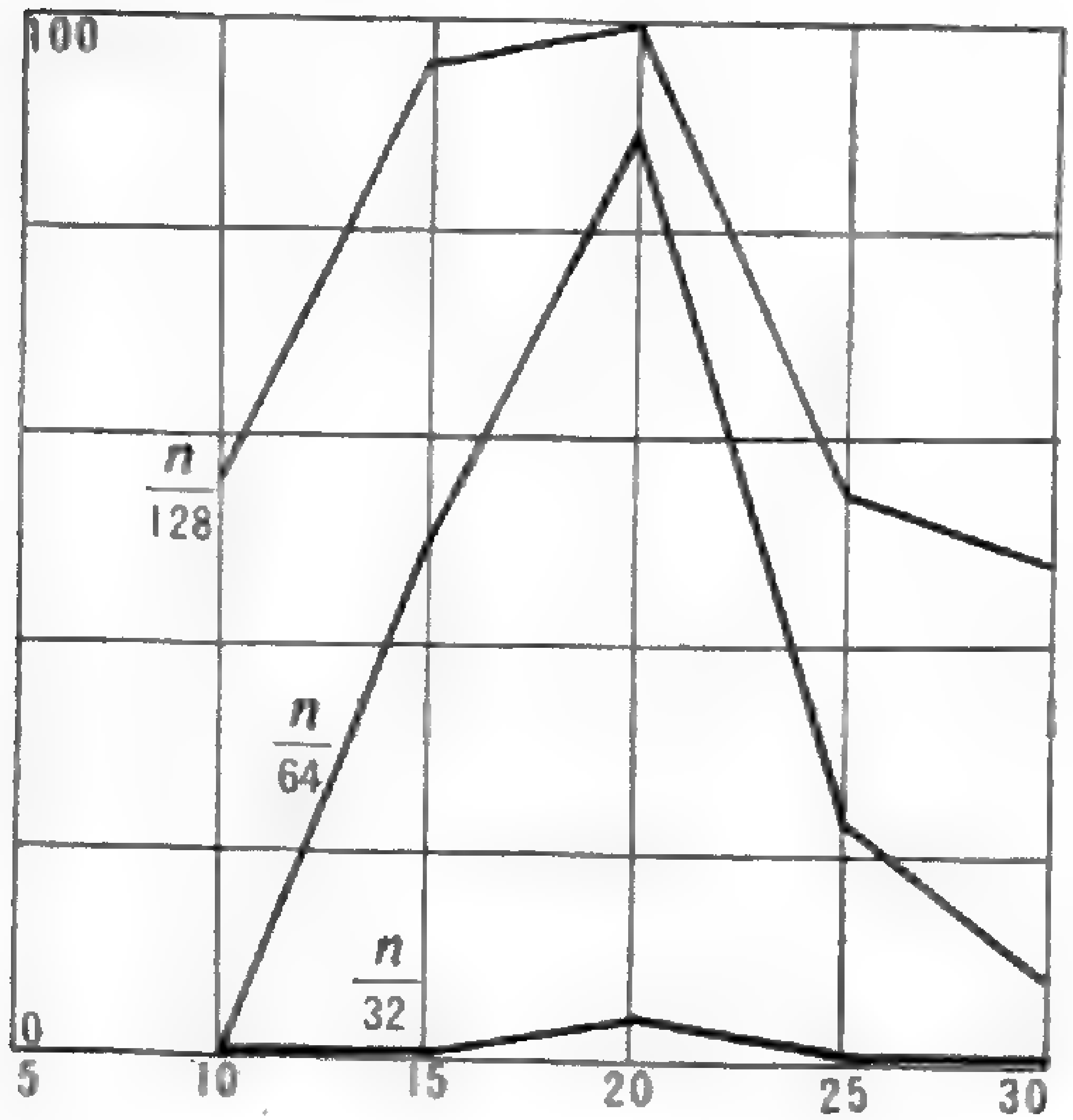


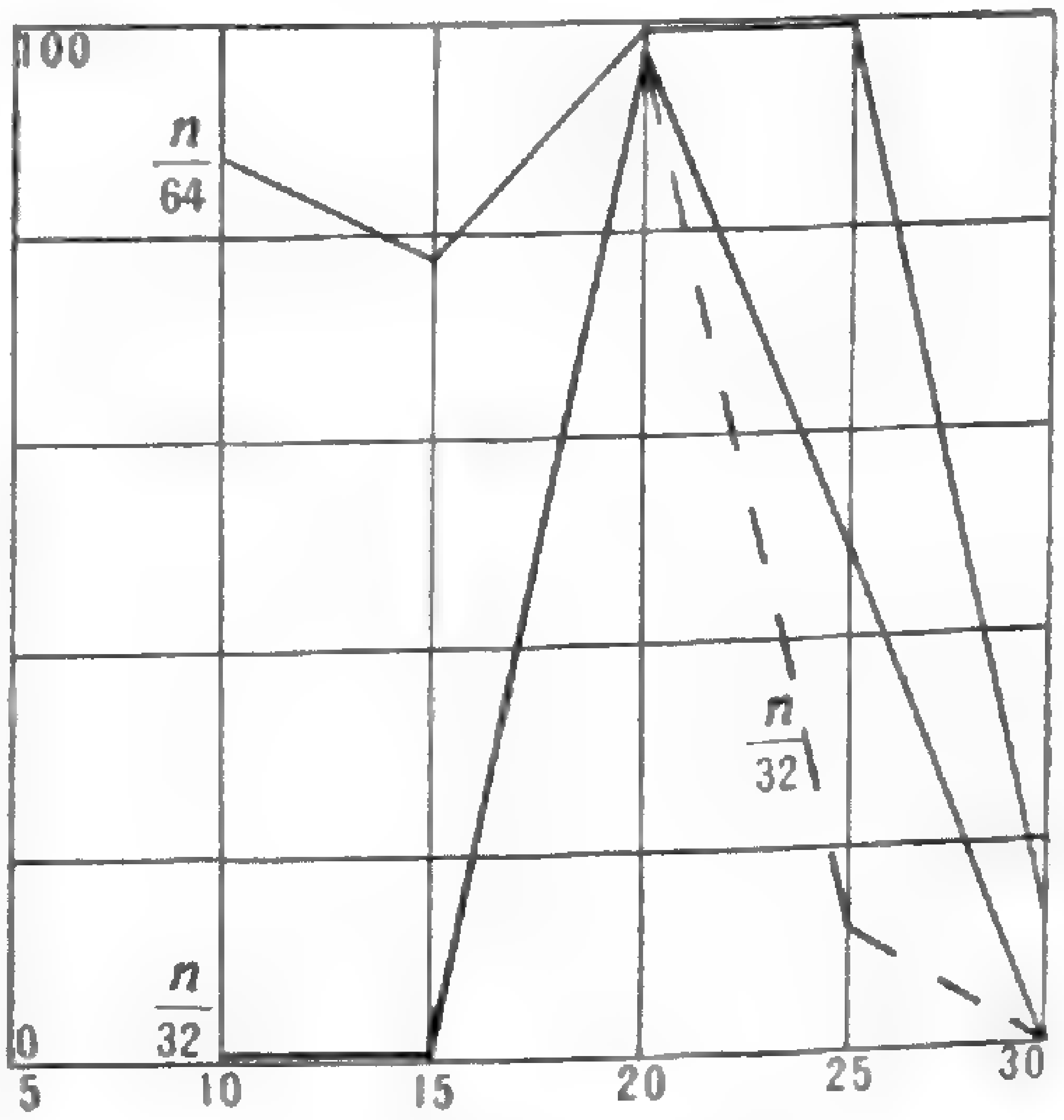
6c, Sterigmatocystis.



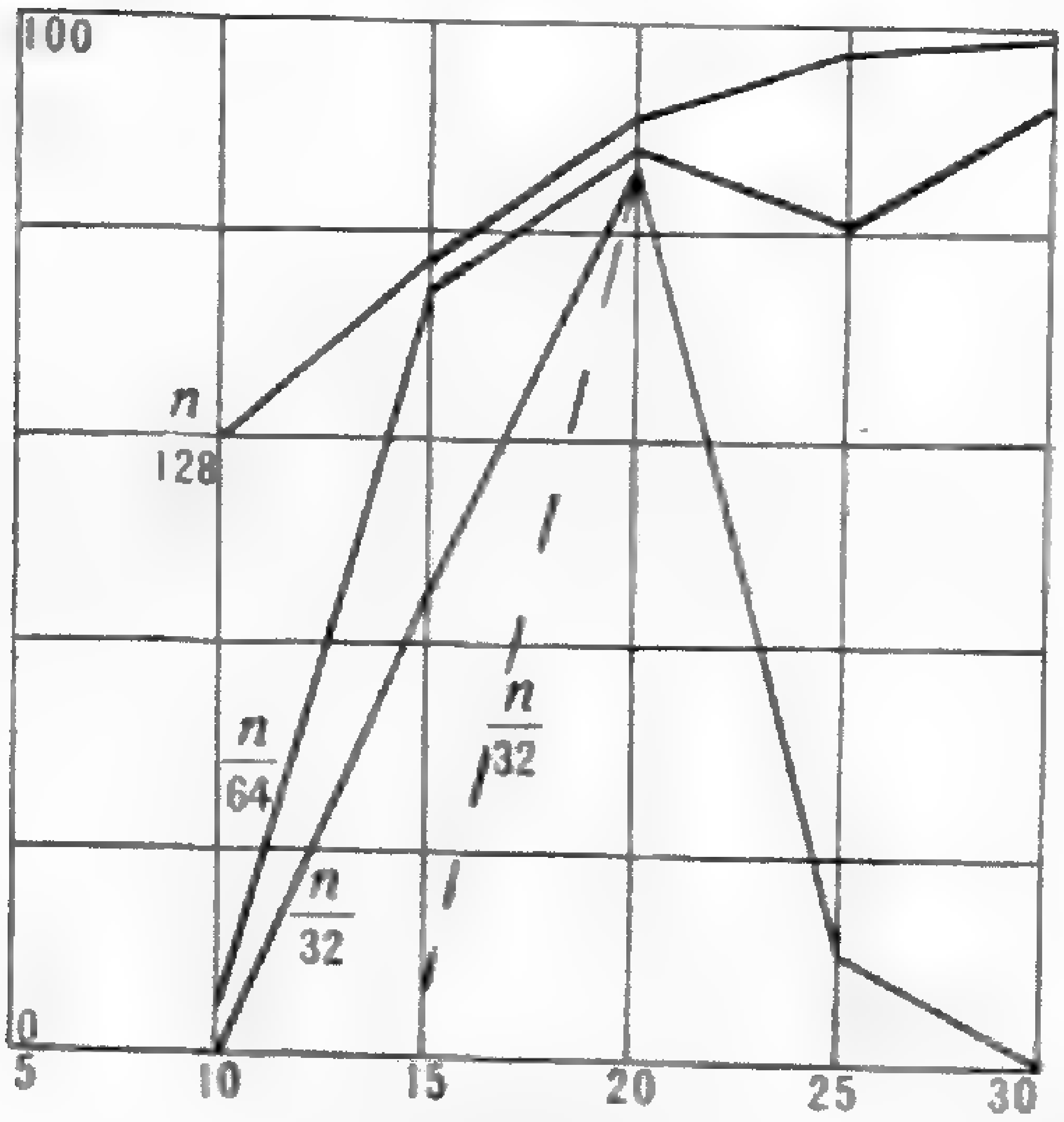


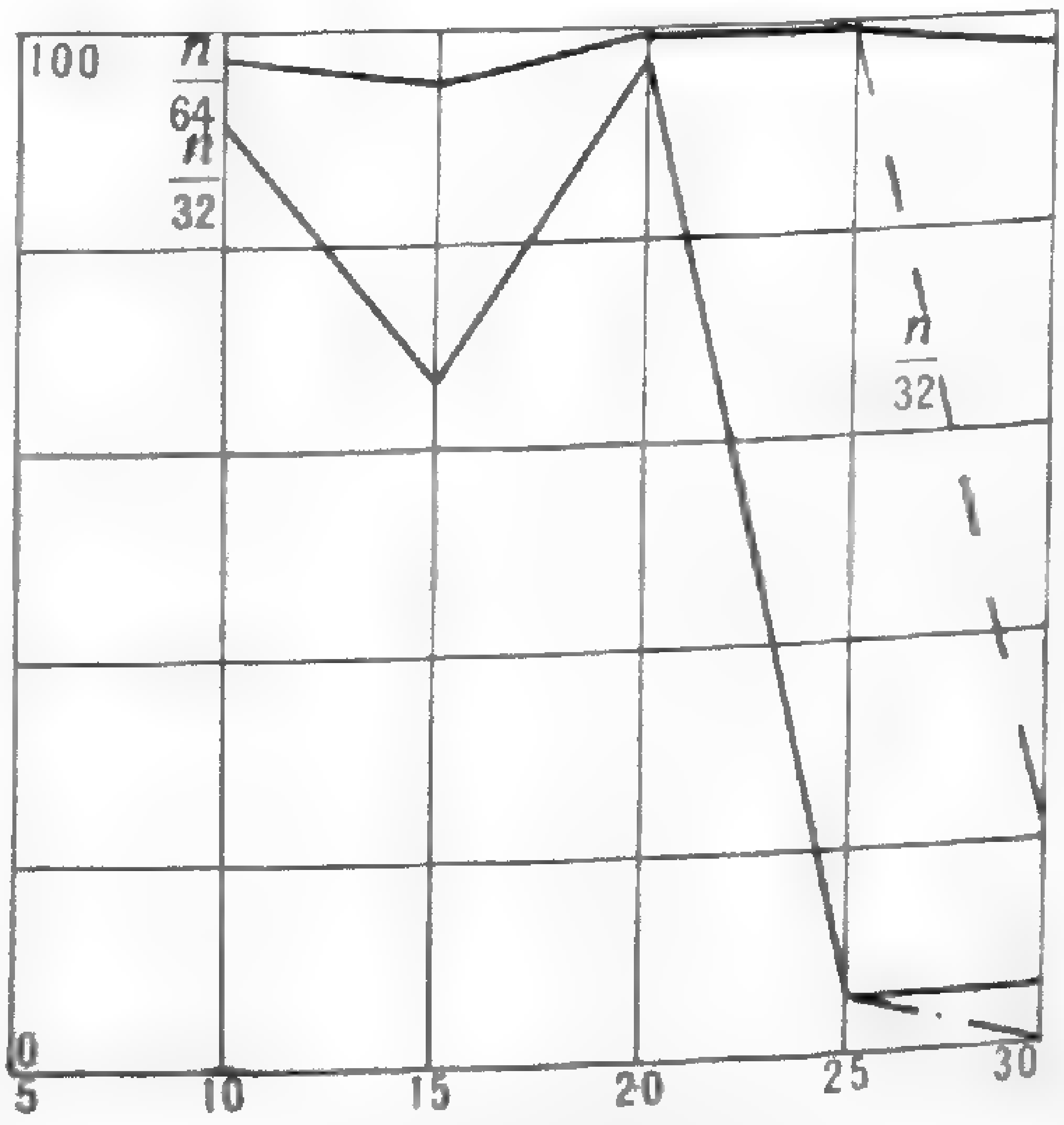
7*a*, Mucor. **$CuSO_4$.** 8*a*, Penicillium.



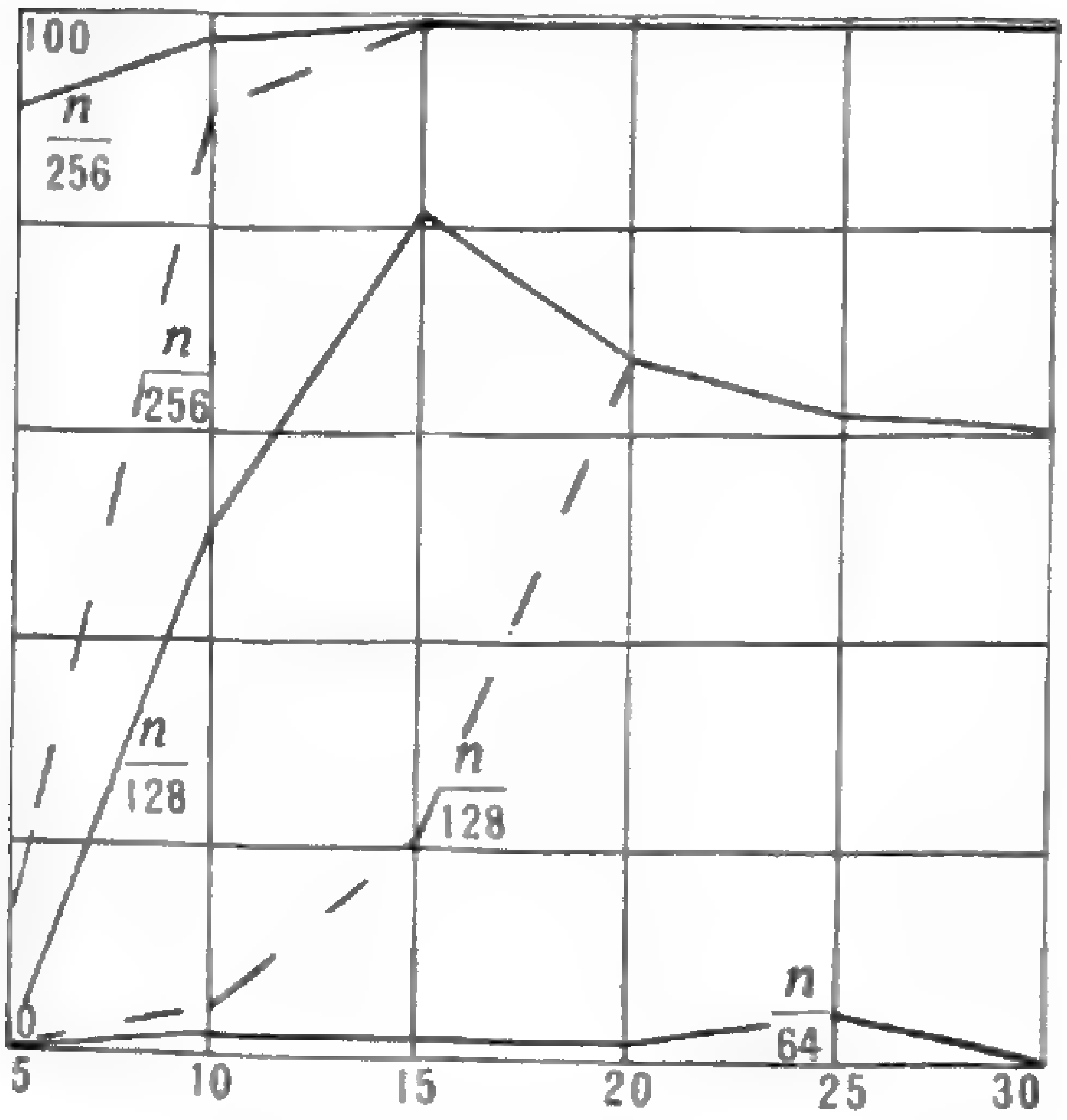


7*b*, Mucor. **H_2SO_4.** 8*b*, Penicillium.



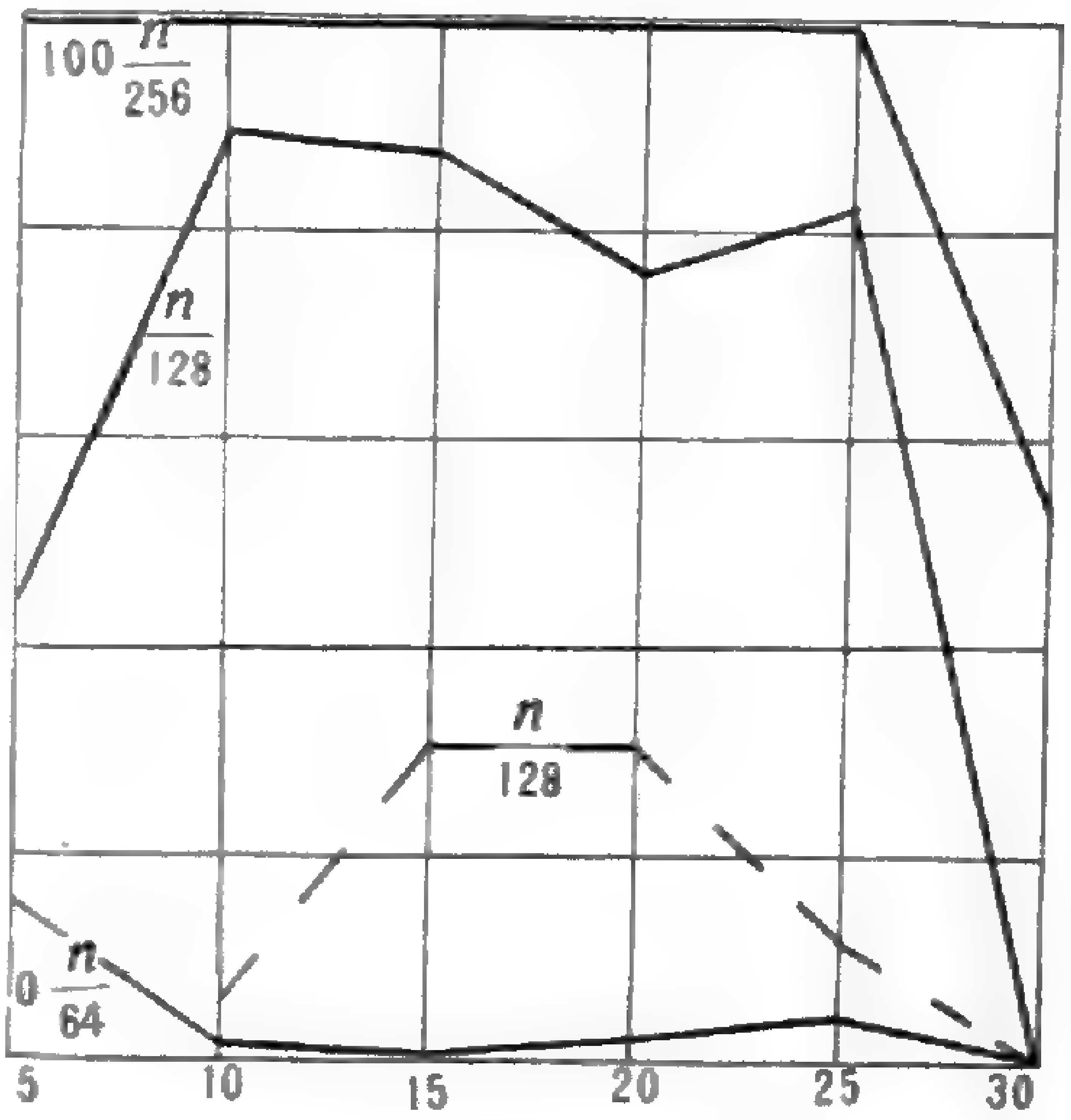


7*c*, Mucor. **HNO_3.** 8*c*, Penicillium.

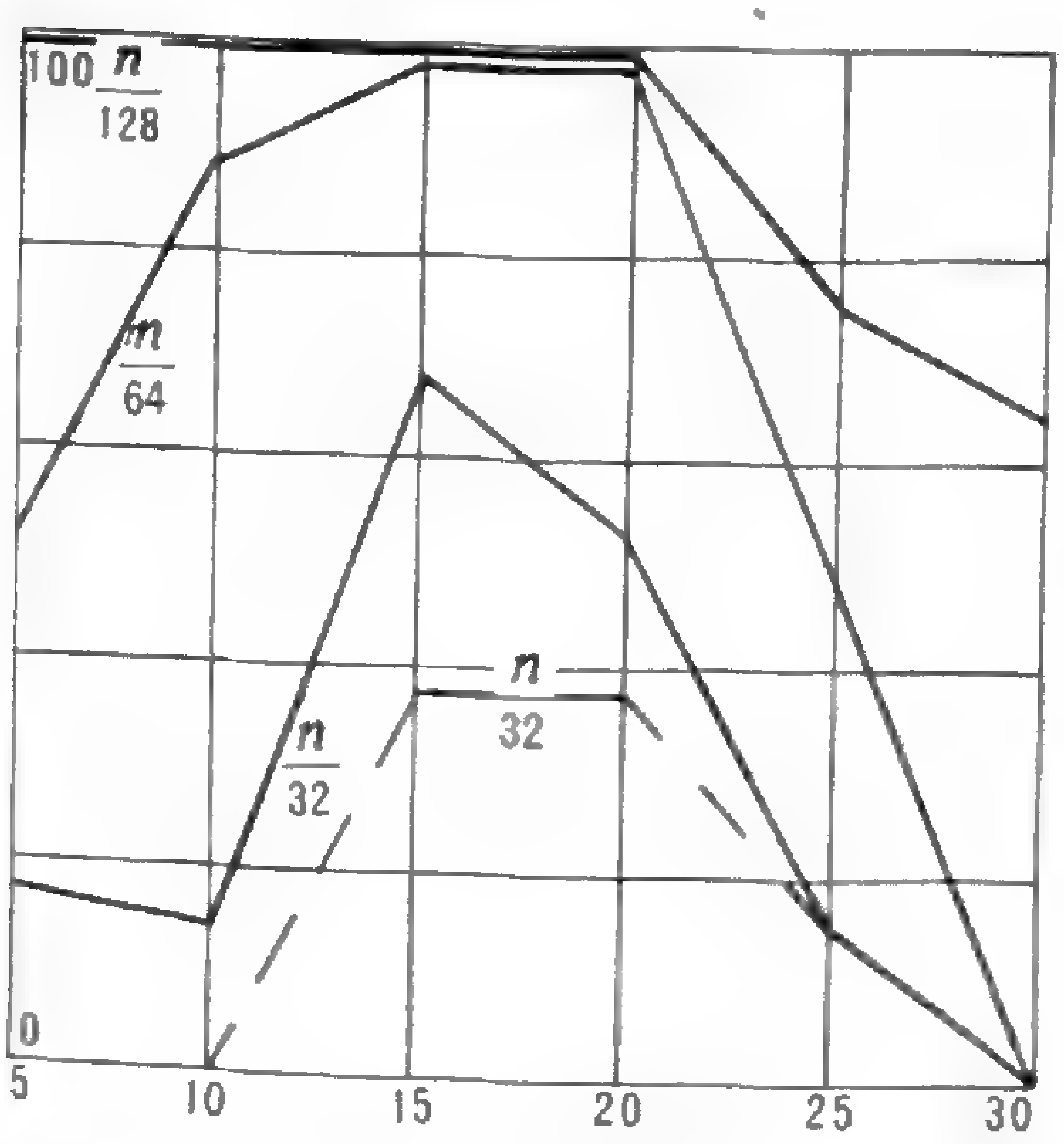


9a, Botrytis.

$CuSO_4$.

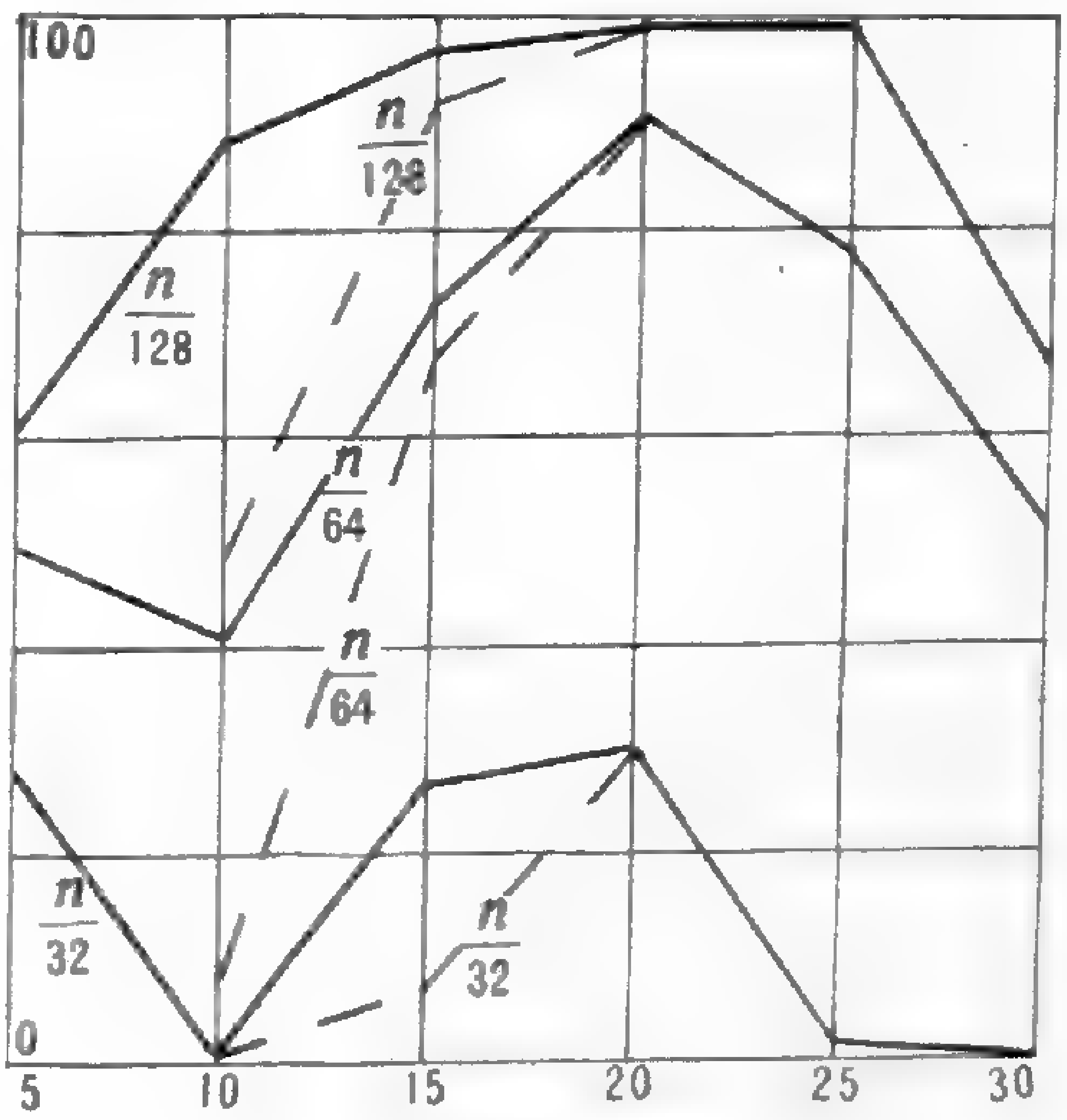


10a, Monilia.

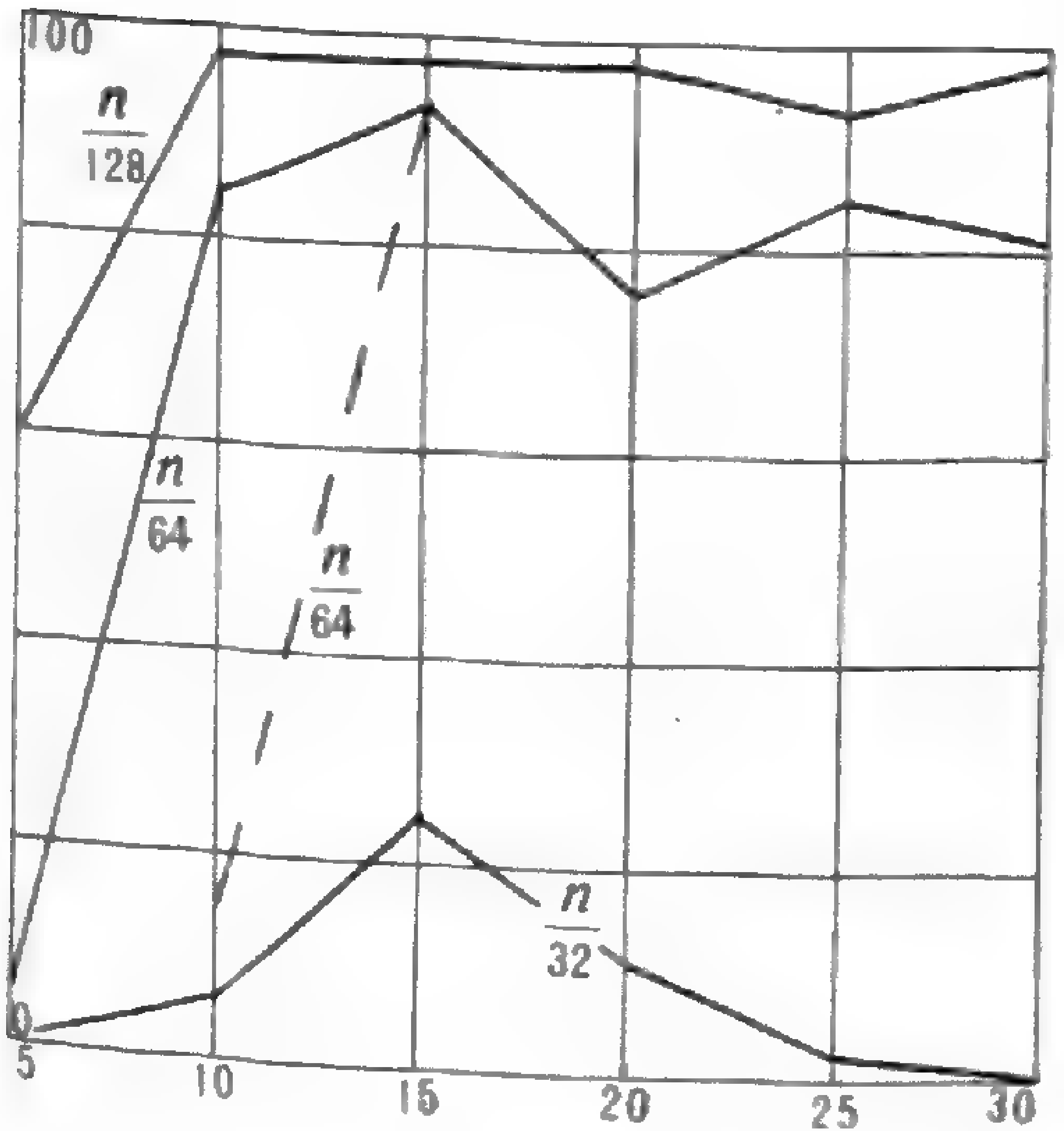


9b, Botrytis.

H_2SO_4.

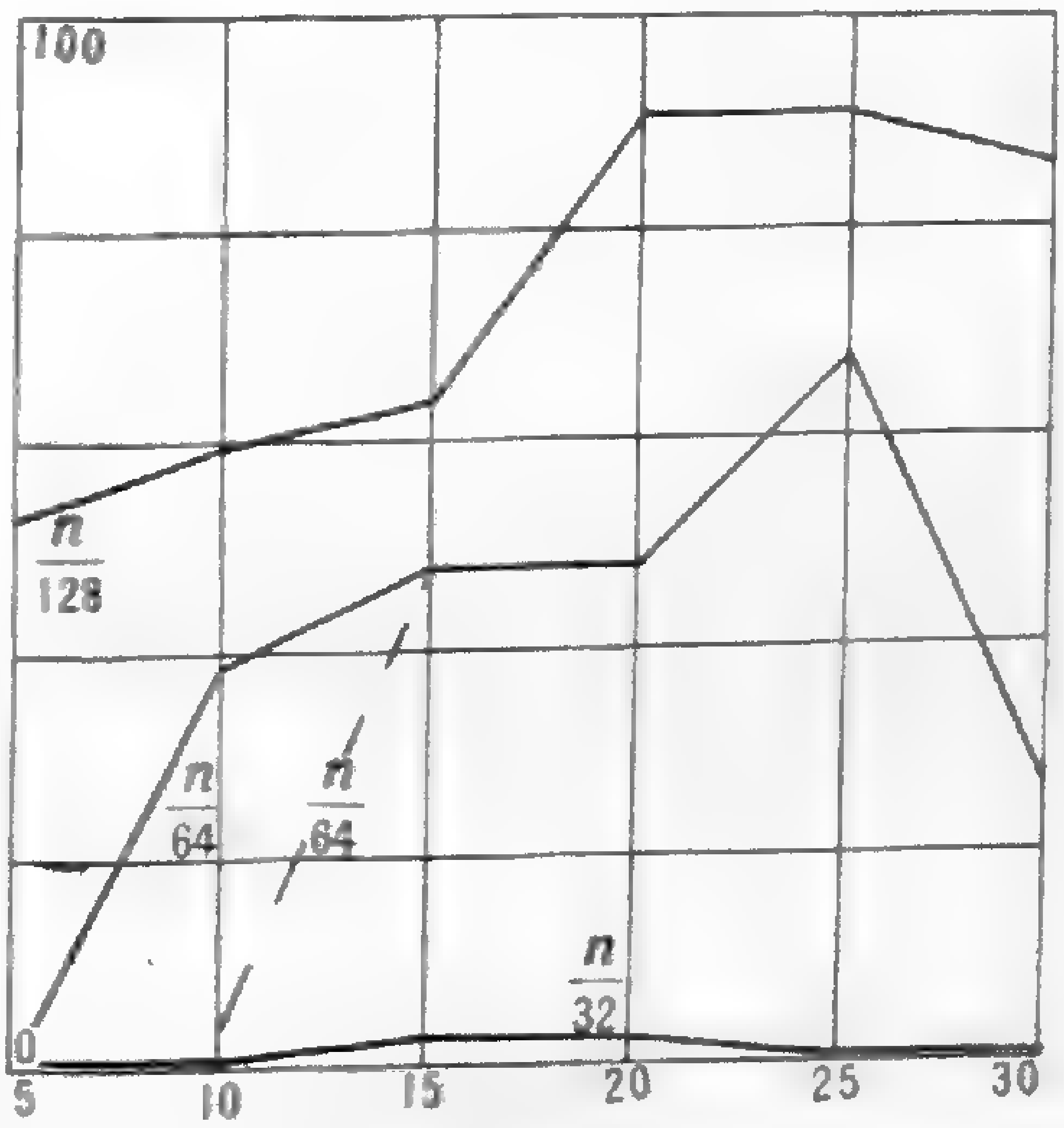


10b, Monilia.



9c, Botrytis.

HNO_3.



10c, Monilia.

at 15° or 20°. This variation may be the result of using solutions that were, without regard to temperature, more injurious to some of the fungi than to others; but strong concentrations, such as *n*/4 and *n*/8 HNO_3, when used with Mucor and Sterigmatocystis, have not given the rise in the curves from 10° to 5° that has been repeatedly obtained with Botrytis and Monilia. It should be noted that these last two fungi are not only the ones that are most greatly injured by the toxic agents, but also are those that require the least stimulus for germination. DUGGAR (**10**) found that both Botrytis and Monilia germinated readily in distilled water, but that Sterigmatocystis and Penicillium did not germinate.

There is also a remarkable agreement in the minimum temperature for the germination of a particular fungus under certain conditions and the location of the fall in its germination curve. Botrytis and Monilia not only show the greatest increase in toxic effect on passing from 5° to 10°, but they are also the only ones that had germinated in the control cultures at 10° by the end of one day. With Penicillium the $CuSO_4$ and HNO_3 curves show a tendency to drop between 10° and 15°, while in the H_2SO_4 curves the fall comes beyond 15°. Along with these data should be noted the fact that the control with the H_2SO_4 cultures gave no germination in one day, while those with the HNO_3 and $CuSO_4$ cultures had germinated in this time. This variation in the controls was probably due to a slight change in the temperature of the refrigerator, together with the fact that 15° approaches the lower limit of temperature for obtaining the germination of Penicillium in one day (WIESNER **13**). Mucor gave no germination the first day in the controls at 15°, with the exception of about 14 per cent. with the $CuSO_4$ series, and Sterigmatocystis in no instance germinated in one day at this temperature. As has been already mentioned, the curves for these fungi fall between 15° and 20° or at a higher temperature. From these facts it is seen that the spores exposed to a harmful agent and at the same time inhibited by cold have not been greatly injured.

In the cultures from which the data in charts *6a* to *10c* inclusive were obtained, the spores were in no instance transferred. The cells in the $CuSO_4$ series remained at the temperature indicated for four days; those with the acids were removed at the end of two days.

In the former six daily observations were made, in the latter only four. Control cultures of spores in beet decoction were kept with the toxic cultures at all times. These controls were subjected to the various temperatures for the same length of time as the other cultures. The per cent. indicated in these charts do not in every instance represent the actual germination, but were in all cases obtained by dividing the per cent. of germination in the particular culture by that in the control at the same temperature. It was found more difficult to represent in graphical manner the results obtained from these experiments, since the per cent. of germination did not always seem to agree with the extent of the injury. The solid lines show the germination at the time of the final removal from the given temperature. The per cent. of germination at the end of twenty-four hours is indicated by the broken lines. These unite with the solid lines as they approach the optimum temperatures. Where no broken line is given the germination was the same at the end of the first day as at the time of removal from the special temperature. The results obtained at temperatures at which the controls had not germinated were omitted from the curves. This accounts for the fact that a number of the curves are not extended to the lower temperatures.

In all instances the injurious effects were least at the optimum for the fungus. This optimum was determined by the germination and development in the controls. The harmful effects were shown by decreased germination as indicated in the charts and by abnormal development. The toxic solutions that gave but partial germination at the optimum for the fungus usually gave only abnormal development above and below that optimum. Thus, Botrytis in $n/32$ HNO_3 gave mycelial development approaching the normal only at 15° and 20°; Penicillium in $n/128$ $CuSO_4$ gave medium growth at 20° but at no other temperature, at 30° the germ tubes seldom became more than a few spore diameters in length even after removal to a more favorable temperature and many spores swelled without germinating. Sterigmatocystis has its optimum above 25° and it is the only fungus in which the injurious effects decreased above that temperature. Both Mucor and Sterigmatocystis germinated and grew well at 35°, the other three fungi gave little or no germination at that temperature.

The charts do not show the results obtained at low temperatures, but in every instance cultures were placed at 5° and 10°. Spores kept for two days in a particular toxic solution at a temperature so cold that it inhibited their germination gave, upon removal to the room temperature, a germination and development that was but little inferior to that obtained from the fresh spores under like conditions of medium and temperature. Spores inhibited at a temperature that did not prevent germination were more greatly injured. Spores of Mucor gave fair growth in $n/32$ H_2SO_4 and $n/32$ HNO_3 after removal from 5°, but after removal from 10° did not germinate. Sterigmatocystis spores in $n/16$ HNO_3 grew almost as well after removal from 10° as from 5°, but in the cultures removed from 15° (a temperature not inhibiting germination in the control) no germination was obtained.

A comparison of the curves obtained with the different chemicals shows that those for weak concentrations of HNO_3 do not drop so rapidly at high temperatures as the curves for weak solutions of the other toxic agents.

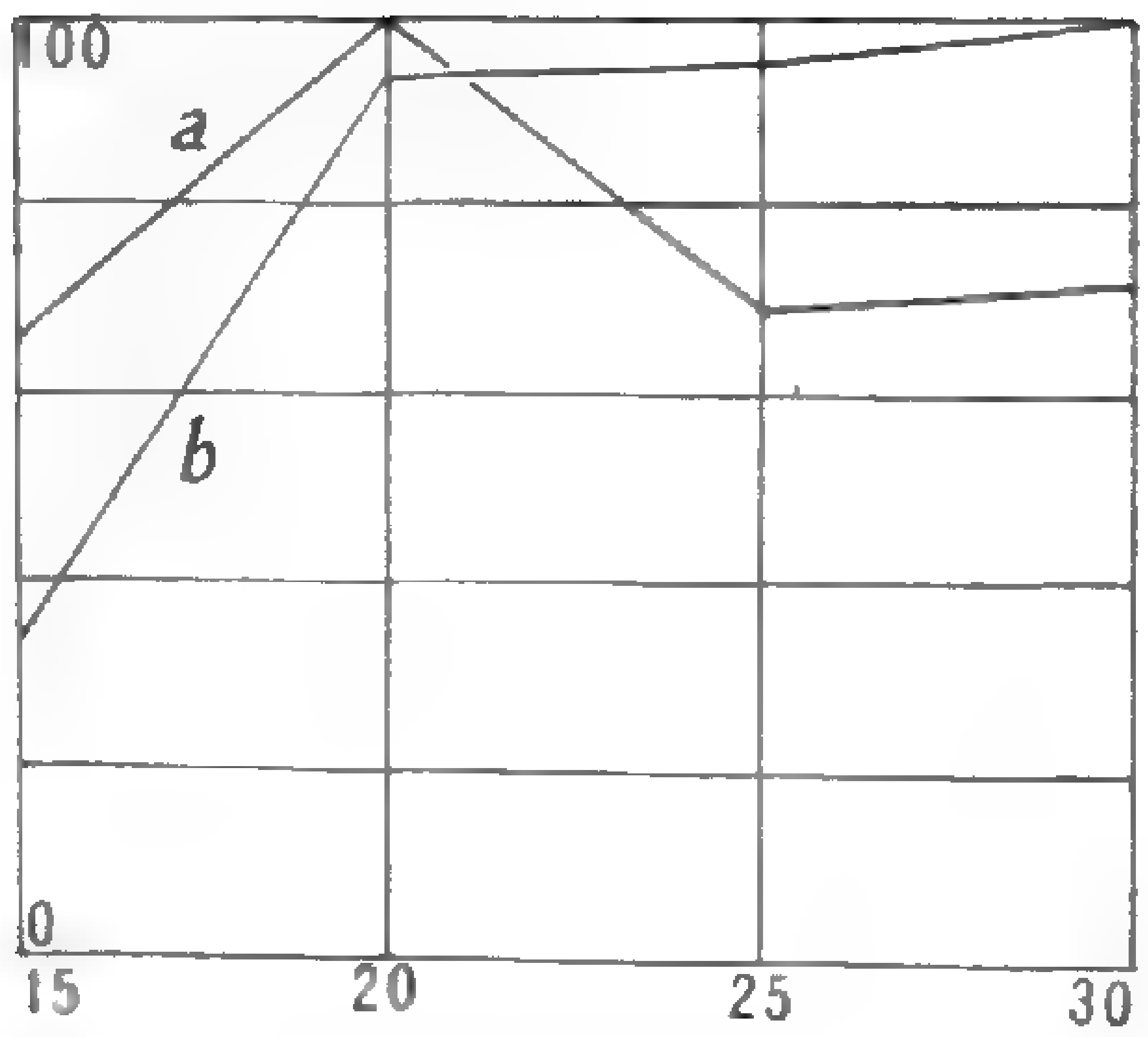
In order to obtain additional information in regard to the significance of the results secured with the cells, a series of flask cultures was made. In every instance 25^{cc} of the given solution were placed in a 100^{cc} flask. These flasks were sterilized after the introduction of the solution. The effect of the toxic agent was determined by taking the dry weight of the fungous growth at the end of the given time. With the exception of $n/64$ $CuSO_4$, duplicate cultures were made and the average weight used in estimating the effect. Flask cultures were made of Mucor, Penicillium, and Sterigmatocystis. The results obtained from cell cultures were used as a basis in determining what strengths of the toxic agents should be used in the flasks. So much greater concentration was required to give injury in flask cultures than in cells that no definite results were obtained with Mucor and Penicillium. Also it was found that Penicillium would not grow in flask cultures placed at 30° C., a temperature at which the fungus grew well in the control cell cultures.

In the series with Sterigmatocystis the air in the incubator was dry, while that in the refrigerator was kept damp by the melting ice. It was feared that the evaporation from the flasks at 25° and 30°

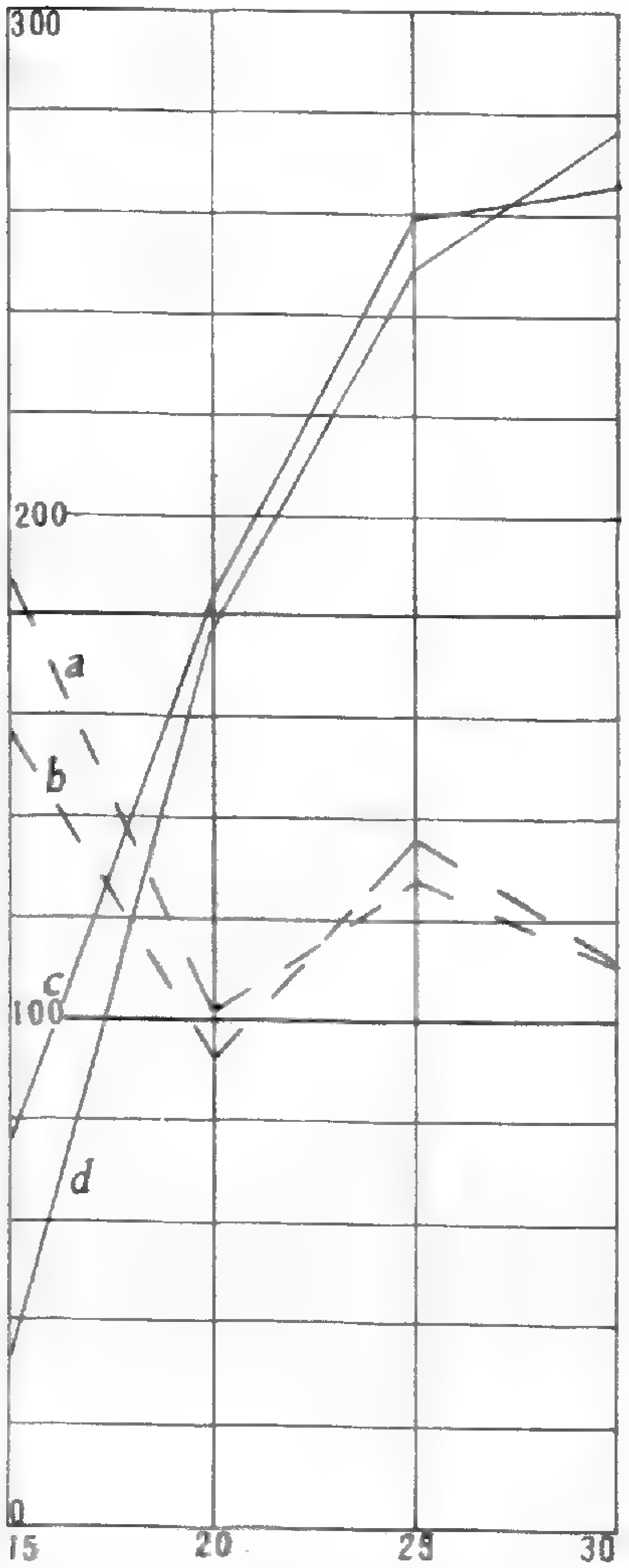
might have been for this reason enough greater than at lower temperatures to cause an appreciable change in the results, and the series was repeated with the hygroscopic conditions more nearly uniform. Charts 12*a* and 11 give the results obtained from the first series, while 11 and 12*b* show the results of the last series. In the first set of experiments the fungus was allowed to grow two weeks, in the last but one week; in the former the cultures for the various temperatures were started at different times, in the latter all were started on the same day and the spores used were from one stock culture.

In charts 11–12*b* the abscissae indicate temperatures as before, but the ordinates express percentages of dry weight instead of percentages of germination. The effect of temperature on the controls is shown in chart 11. In this chart the curves were determined by taking the greatest dry weight as 100 and estimating what per cent. of this the weights secured at other temperatures were. In charts 12*a* and 12*b* these same controls are represented by the ordinates marked 100. In plotting the curves of these two charts, the weight of fungus secured in a given toxic solution at a particular temperature was compared in each case with the weight obtained in the control at the same temperature. The results thus obtained are expressed by the ordinates as mentioned above.

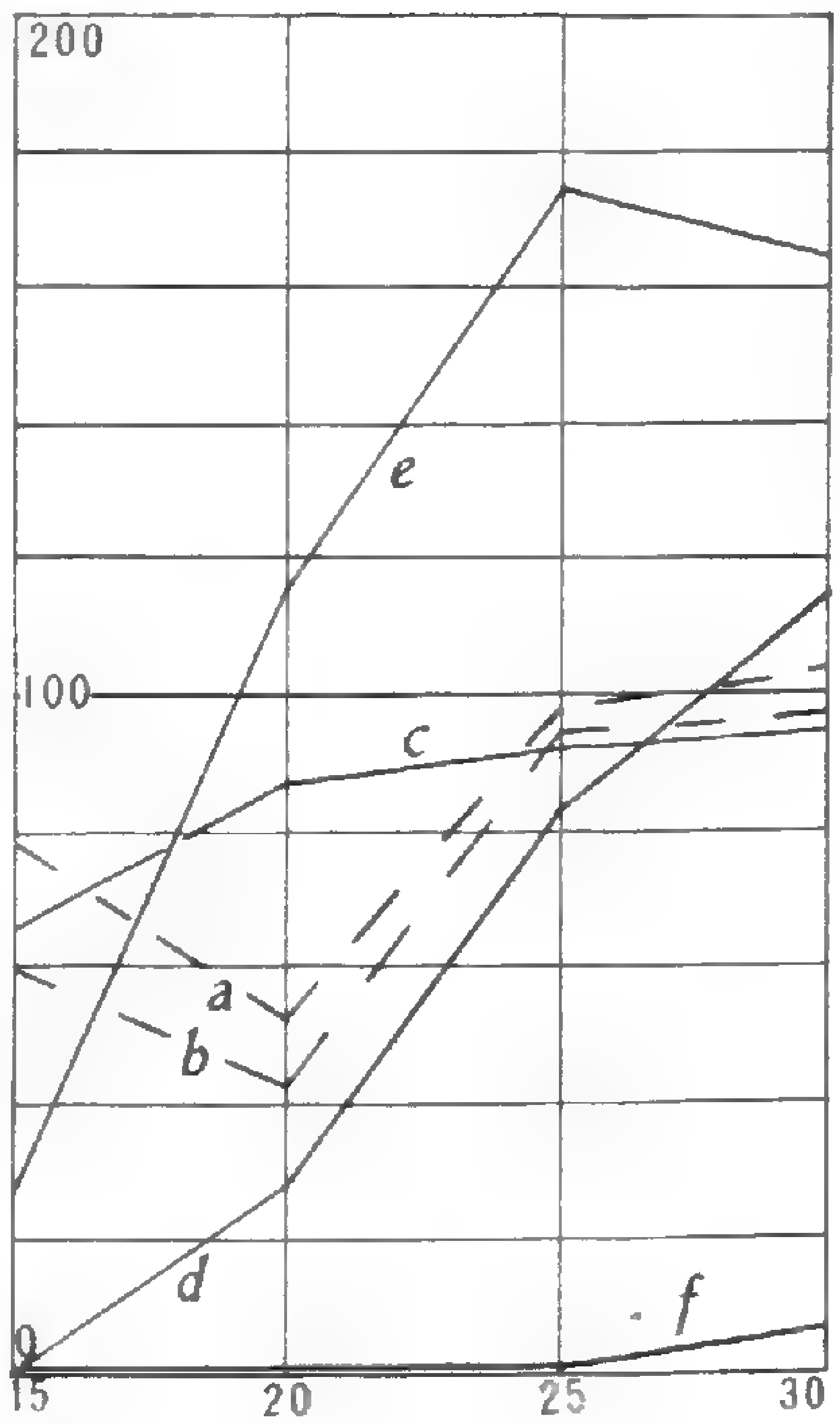
It will be seen that in most instances the curves in the two charts are in close agreement. Where this is not true, as in the case of the controls, the results obtained in the last series should be considered the more reliable for the reason previously given. Taking total growth as a standard, the injurious effects of the toxic agent have decreased with rise of temperature. This decrease is rather to be considered as the result of approaching the optimum for the fungus than as a mere temperature effect. The effects produced by the three chemicals were widely different. The injury resulting in the $CuSO_4$ solutions was not so great, comparatively. at 15° as at 20°. This was true of neither of the acids. Sulfuric acid checked the growth at the lower temperatures, but in no case served as a strong stimulating agent. Nitric acid gave similar injurious effects, but at the higher temperatures served as a remarkable stimulus. It should be remembered that a similar rise at 25° and 30° was obtained in the cell culture curves for HNO_3.



11, Sterigmatocystis. Control curves; *a*, for first series; *b*, for second series.



12*a*, Sterigmatocystis, first series. *a*, *n*/256 $CuSO_4$; *b*, *n*/192 $CuSO_4$; *c*, *n*/32 HNO_3; *d*, *n*/24 HNO_3.



12*b*, Sterigmatocystis, second series. *a*, *n*/128 $CuSO_4$; *b*, *n*/64 $CuSO_4$; *c*, *n*/20 H_2SO_4; *d*, *n*/10 H_2SO_4; *e*, *n*/20 HNO_3; *f*, *n*/10 HNO_3.

The writer hopes by means of further experiments to be able to obtain additional information in regard to the meaning of the difference in action of the chemicals and the significance of the varying effects upon the different fungi. He wishes to acknowledge his indebtedness to Dr. B. M. Duggar, Professor of Botany in the University of Missouri, for suggesting the problem reported upon in this paper and for valuable advice throughout the prosecution of the work.

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Durham, N. H.

LITERATURE CITED.

1. THIELE, Die Temperaturgrenzen d. Schimmelpilze 10, 36. 1896.
2. NÄGELI, Die niederen Pilze 30, 200. 1877.
3. HEIDER, Ueber die Wirksamkeit von Desinfektionsmitteln bei höherer Temperatur. Cent. Bakt. **9**: 221–228. 1891.
4. PASTEUR, Compt. Rend. **84**: 206. 1877.
5. COHN, Beitr. z. Biol. Pfl. **2**: 255, 259. 1877.
6. BREFELD, Unters. ü. d. Spaltpilze 10. 1878.
7. RICHET, C., La chaleur animale. Paris. 1889.
8. MATHEWS, A. P., The relation between solution tension, atomic volume, and the physiological reaction of the elements. Amer. Jour. Physiol. **10**: 290–323. 1904.
9. CLARK, J. F., On the toxic effect of deleterious agents on the germination and development of certain filamentous fungi. BOT. GAZETTE **28**: 289, 378. 1899.
10. DUGGAR, B. M., Physiological studies with reference to the germination of certain fungous spores. BOT. GAZETTE **31**: 38. 1901.
11. FERGUSON, MARGARET C., A preliminary study of the germination of the spores of *Agaricus campestris* and other basidiomycetous fungi. U. S. Dept. Agric., Bureau Pl. Ind., Bull. 16. 1902.
12. CLARK, J. F., On the toxic properties of some copper compounds with special reference to Bordeaux mixtures. BOT. GAZETTE **33**: 26. 1902.
13. WIESNER, J., Untersuchungen über den Einfluss der Temperatur auf die Entwicklung des *Penicillium glaucum*. Sb. Wien. Akad. **68**: 5–16. 1873.

THE EMBRYOGENY OF SOME CUBAN NYMPHAEACEAE.

MELVILLE THURSTON COOK.

(WITH PLATES XVI–XVIII.)

THE taxonomic position of the Nymphaeaceae has always been somewhat doubtful. The anatomy of these plants is more nearly that of the monocotyledons, while the venation of the leaves would indicate that they are dicotyledons. A few years ago researches in this family were stimulated by LYON'S studies (**17**, **18**) on the embryogeny of Nelumbo, in which he came to the conclusion that they should be classified among the monocotyledonous families in the series Helobiae. LYON'S views were strengthened by my own paper on the embryogeny of *Castalia odorata* and *Nymphaea advena* (**7**), by SCHAFFNER'S paper on morphological peculiarities of the Nymphaeaceae and Helobiae (**26**), and by YORK'S embryological studies on Nelumbo (**28**). But CONARD (**5**, **6**) in his studies in this same family took exceptions to this view, and holds to the idea that they should be classified among the dicotyledons. More recently, MOTTIER (**20**) has declared his belief that they are anomalous dicotyledons. However, he does not claim to have made any study of the Nymphaeaceae, but confines his studies to well recognized dicotyledonous species.

Immediately following LYON'S paper (**18**) on the embryogeny of Nelumbo, CAMPBELL (**4**) raised the question as to whether other genera of the Nymphaeaceae might not also be monocotyledonous, and called attention to the fact that the structure of the flowers and character and arrangement of the vascular bundles in Cabomba and Brasenia were very similar to some of the Alismales; also "that the form of the leaves is often very suggestive of the sagittate leaves of Alisma or Sagittaria."

In consideration of the differences of opinion indicated above the writer accepted an opportunity to make a study of certain tropical species, hoping that additional light might be thrown on this very interesting family.

SCHAFFNER (**26**) called attention to the fact that it is in reality much easier to read monocotyledonous than dicotyledonous characters into the flowers; that while the genus Castalia has been described as having four sepals, *C. odorata* usually has only three, though sometimes by an expansion of the receptacle one segment of the second cycle is more or less exposed, while in *C. tuberosa* the displacement is normal. This led me to make a similar study of *C. pubescens*. In this species I found that 80 per cent. have the first segment of the second cycle exposed, while 20 per cent. have the second segment of the second cycle more or less exposed, thus showing five parts. SCHAFFNER also called attention to certain other secondary resemblances, such as number and arrangement of ovules and ovularies, between the Nymphaeaceae and well-recognized monocotyledonous plants.

The vascular bundles of all the species referred to in this paper were also studied, but gave no facts other than those already well-known, the bundles in all cases being of the well-recognized closed type and arranged in the stems after the usual manner of this family.

On account of the large amount of gummy substance surrounding the ovules, considerable difficulty was experienced in getting a killing fluid to penetrate. This was especially true for *Brasenia purpurea* where the gummy substance was most abundant. Picric-acetic solutions proved to be the best fixing agents, while chrom-acetic and the Flemming's solutions were unsatisfactory and could be used only for the development of the embryo sac and the stamens.

THE EMBRYO SAC.

The formation of the embryo sacs in all genera is very similar, and in fact practically the same as described in my first paper (**7**). I will not give a discussion of each, therefore, but will give a general outline and present a series of figures illustrating the more important points, with special attention to the mature sac and the changes at the time of fertilization and immediately following.

The archesporial cell develops from the hypodermis (*fig. 11*) and is easily recognized. An indefinite number of tapetal cells, usually varying from four to eight, are then produced. Three or four megaspores are then formed. The four may be produced either by a regular division of the mother cell into four cells; or occasionally by the division of the mother cell into three cells, followed by a division of the middle one (*fig. 2*).

The innermost megaspore is functional and develops rapidly into the embryo sac at the expense of the other megaspores and the tapetal cells. This enlarged cell (*fig. 3*) now touches the epidermis at the micropyle and passes rapidly through the two-, four-, and eight-nucleate stages. The mature embryo sac is very small and straight, and the enlargement is principally in the direction of the long axis of the ovule. Starch is usually very abundant and persists throughout the two- and four-nucleate stages, and in *Brasenia purpurea* and *Cabomba piauhiensis* usually throughout the eight-nucleate stage. It gradually disappears, first from the micropylar end of the sac and finally from the antipodal end (*fig. 6*). It probably undergoes modification to form the first food for the development of the embryo and endosperm.

Occasionally two embryo sacs were produced, but one was always absorbed by the other (*fig. 7*). This was more frequent in *Cabomba piauhiensis* than in any other species studied. Fertilization occurs almost immediately upon the completion of the eight-nucleate stage of the sac. The same very pronounced sclerification of the inner part of the epidermal cells (*fig. 4*), previously observed by me (**7**) for *Castalia odorata*, was observed in the tropical species of Castalia studied, but not in the other genera. The actual penetration of this epidermal wall by the pollen tube was observed in only a few cases. In fertilization the pollen tube (*fig. 4*) enlarged and stained so deeply that it was impossible to observe what fusion of nuclei did occur. At the time of fertilization the polar nuclei are very large, usually rather indistinct, and unite at the micropylar end of the sac just below the egg apparatus. At the same time the antipodals, which are very inconspicuous, undergo degeneration (*fig. 4*). The synergids may persist a short time after fertilization (*figs. 5, 6, 7*), but usually disappear very quickly. They are most persistent in *Cabomba piauhiensis.*

The primary endosperm nucleus, which is now very large and conspicuous, moves to the antidopal end of the sac (*figs. 5, 6*), where it divides (*figs. 7, 8, 20*), and a very delicate wall is formed across the sac between the two daughter nuclei. This wall can be observed without great difficulty in *Nymphaea advena* (*fig. 8*) and in *Castalia ampla* (*fig. 20*), but is very difficult to see in the other species studied.

The nucleus next to the embryo divides repeatedly, thus forming the endosperm which will be described later. The nucleus in the antipodal end acts slightly differently in the different species and will hereafter be designated the nucleus of the nucellar tube.

In *Nymphaea advena* a long tube-like extension of the sac is now formed through the nucellus, beginning with the antipodal end of the sac and extending to the chalazal end of the ovule. The very large and conspicuous daughter nucleus of the antipodal end, formed by the division of the endosperm nucleus, enters this tube, which will be called the nucellar tube, and travels to the chalazal end of the ovule, where it undergoes disintegration (*figs. 8, 12, 13, 14*). When the embryo is in the two-celled stage, the tube and nucleus have traveled about two-thirds the length of the ovule (*figs. 8, 12*); and when the embryo has reached the quadrant or octant stage, the tube is complete (*figs. 13a, 13b*). In one case only (*fig. 13b*) the tube nucleus had divided. After this time it disintegrates (*fig. 14*). In its early development the tube is filled with protoplasm which to all appearances is traveling towards the embryo sac. This is exactly the condition observed by me in *Nymphaea advena* and *Castalia odorata* and described in my first paper (**7**).

In *Castalia ampla* (*fig. 20*) the nucellar tube is a short thick sac which is separated from the embryo sac by a constriction and by a thin wall, and which contains a very large nucleus and a large amount of protoplasm. As the embryo increases in size, the embryo sac enlarges, encroaching upon this nucellar tube sac and absorbing its contents (*fig. 21*). The formation of this tube sac is very similar to that described by JOHNSON (**12**) for *Saururus cernuus*, except that in that species the tube sac is relatively larger and persists in the mature seed.

In *Castalia pubescens* the nucellar tube is much slower in development, much less conspicuous, and apparently of much less importance than in any of the other species studied. Extending from the antipodal end of the sac to the chalazal end of the ovule is a great mass of elongated cells (*fig. 24*) which are much richer in protoplasmic contents than the other cells of the nucleus. The greater part of this mass of cells disintegrates slowly and thus is formed a small tube reaching usually not more than one-half the length of the ovule (*fig. 9a*). The tube is flat (*fig. 9b*) instead of cylindrical as in the case of the other species. This tube is usually completed just before the appearance of the cotyledonary ridge of the embryo. The nucleus was observed in the antipodal end of this tube but apparently disintegrated, and did not pass to the opposite end of the tube as in the case of the other species.

In *Brasenia purpurea* and *Cabomba piauhiensis*, the nucellar tube is long but very small. There is a rapid disintegration of the nucellar tissue to form the tube before the tube nucleus begins its passage. The tube nucleus gradually disintegrates, and has entirely disappeared before it reaches the chalazal end of the tube (*figs. 7, 10, 11*); the chalazal end of the tube is considerably enlarged, is not so definite in outline as in *Nymphaea advena*, and contains fragments of the cell walls (*fig. 11*).

In my previous discussion (**7**) I called attention to the fact that the behavior of the endosperm nucleus is similar to that of *Sagittaria variabilis* as described by SCHAFFNER (**25**), except that in *S. variabilis* there is no nucellar tube elongation; also, that judging from the studies of WIEGAND (**27**) and HOLFERTY (**10**) on Potamogeton it is possible that a similar condition may be found in that genus.

Since that time, HALL (**9**), in his studies on *Limnocharis emarginata*, in which he finds a single polar nucleus, says:

> The upper polar nucleus, when it has approached the antipodal end of the sac, divides transversely. The lower daughter nucleus remains in the position of its formation, being cut off by a wall across the sac and forming a large cell which does not divide further, but finally disappears through the encroachment of the endosperm. . . . . The upper daughter nucleus travels back towards the egg apparatus, and by its further division forms the endosperm.

STRASBURGER (**23**) describes a similar action of the endosperm nucleus of *Ceratophyllum submersum*, in which, after the first division, the nucleus in the antipodal end of the sac does not divide, while the nucleus of the micropylar end forms the endosperm.

CAMPBELL (**1**) in his discussion of *Naias flexilis* and *Zannichellia palustris* describes a condition which further study may prove to be similar to the Nymphaeaceae. In discussing Naias he says:

> A peculiarity noted, which was also observed in Zannichellia, was the presence of a single large nucleus close to the antipodals, which was conspicuous at an early period and behaved much like the nucleus of the suspensor. Whether this

> was the lower polar nucleus or one of the two endosperm nuclei resulting from the first division of the primary endosperm nucleus could not be determined. Whichever is the case, it never divides, and all the endosperm nuclei arise from the division of the other primary endosperm (or polar) nucleus. The endosperm is limited, there being usually no trace of cell formation.

In discussing *Zannichellia palustris* he says:

> As in Naias, there is evident soon after fertilization a large nucleus just above the antipodal cells, which undergoes no division, but increases very much in size. This is more variable in size than in Naias; not infrequently it could not be detected in the later stages, and in several instances it looked as if it were undergoing disintegration.

Previous to this time, JOHNSON (**12**) had published his studies on *Saururus cernuus*, in which he described a division and behavior of the endosperm nucleus very similar to what I described for Nymphaeaceae, and the formation of a nucellar tube sac intermediate between what I have described in this paper for *Nymphaea advena*(?) and *Castalia ampla*. JOHNSON (**15**) has since called attention to other genera of the Saururaceae (Anemiopsis and Houttuynia) which possess this character.

In my previous discussion of this subject (**7**), I expressed the opinion that the physiological significance of this nucellar tube and nucleus presented a very interesting problem, which should be considered in connection with the function of the antipodals. I called attention to the fact that in Ranunculaceae, Sparganium, and Vaillantia the antipodals appeared to furnish nourishment for the embryo; that the peculiar haustorial development of the antipodals of Vaillantia, the enlargement of the lower antipodal in Aster, the accumulation of endosperm in the antipodal region of Alyssum, and the large lower nucleus formed by a division of the endosperm nucleus (nucellar tube nucleus) in Sagittaria and the Nymphaeaceae showed a resemblance which I believed to indicate a similar physiological function. At about the same time IKEDA (**11**) published the results of his studies on the physiological functions of the antipodals, in which he demonstrated by microchemical observations that the antipodals of Liliaceae possessed very important physiological functions.

JOHNSON (**14**) also considers the antipodals of considerable physiological importance in certain of the Piperaceae, in which he describes them as increasing in size and sometimes in number. It seems very evident that this nucellar tube and its nucleus, which has common origin with the endosperm nuclei, are important structures for supplying food to the embryo through the agency of the endosperm. In *Castalia pubescens*, where the tube is developed, the same function is performed, first by the axial core of elongated cells (*fig. 24*) and later by the small nucellar tube (*fig. 9*).

York (**28**) in his studies on Nelumbo did not observe the formation of a nucellar tube with its nucleus, but claims that both nuclei formed by the first division of the primary endosperm nucleus divided repeatedly. However, it may be that York failed to observe the first division of this endosperm nucleus, that the tube nucleus disintegrates very quickly as in *Castalia pubescens*, and that he really observed the secondary divisions of the daughter endosperm nucleus in the micropylar end of the sac.

ENDOSPERM.

The development of the endosperm in this family presents two distinct types, Nymphaea, Castalia, and Nelumbo illustrating one, and Brasenia and Cabomba the other. The first type shows the formation of cell walls, that is, a cellular endosperm throughout its entire development; while the second type forms cell walls only in the latter part of its development. The formation of the two types of endosperm by closely related plants has been noted by several investigators.

In the first type the first cell walls are formed across the sac (*figs. 13a, 20, 23*), but gradually become more irregular and extend in various planes (*figs. 21, 24, 25*). At first the cells contain considerable protoplasm and the entire endosperm is very active, but in a short time it seems to have reached its maximum activity and importance. In *Castalia pubescens*, at about the time and following the appearance of the cotyledonary ridge, the endosperm cells immediately over the plumule show a marked difference from the surrounding cells (*fig. 9a, x*). They are slightly smaller, more delicate, and are probably the cells which give nourishment directly to the embryo. In this same species the endosperm may penetrate the antipodal end of the nucellar tube a short distance (*fig. 23*).

In the second type, represented by Brasenia and Cabomba, the protoplasm is very dense and the cells at first divide rapidly, but no cell walls are formed (*figs. 10, 33b*). After the embryo has passed the stage indicated in *fig. 34*, the endosperm appears to become thinner and does not stain readily until the embryo is near maturity. The protoplasm then becomes very dense, cell walls are formed, and one layer (occasionally two or three in Brasenia) of cells is developed which completely surrounds the embryo (*fig. 40*). This endosperm is usually thicker and forms two or more layers in a zone around the embryo at the point of origin of the cotyledonary lobes (*fig. 38, x*), and are very thin just below the root tip (*fig. 38, y*). It appears that the endosperm in Brasenia and Cabomba must perform a more important function in the germination of the embryo than in the species of the other genera.

JOHNSON (**14**) in his studies on Piperaceae has expressed the opinion that the "embryo sporophyte of the second generation is never nourished by the parent sporophyte directly, but always through the intermediate gametophyte." The development and action of the endosperm in Nymphaeaceae confirms JOHNSON'S conclusions.

In all species studied there is a pronounced lateral enlargement of the embryo sac, at the expense of the nucellus, to accommodate the increasing endosperm and growing embryo (compare *figs. 24* and *25*).

EMBRYO.

The development of the embryo shows a very wide range of variation. The embryo of *Nymphaea advena* (?) of Cuba follows almost exactly the same course as previously described by the writer for *Nymphaea advena* of the northern United States. The fertilized egg first divides transversely (*fig. 12*), and then two longitudinal walls result in a spherical embryo of eight cells. Successive cell divisions occur, but the spherical character is retained for some time, after which there is an excessive growth on the side next to the micropyle, forming a suspensor by which the embryo is attached to the nucellus, and a flattening on the opposite side, thus giving the embryo the shape of a short blunt cone, or rather of a pear (*fig. 16*). In this respect it differs from *N. advena* of the north, in which the suspensor is much more rudimentary and does not develop until much later. At this time it somewhat resembles the embryo of *Sparganium simplex* as described by CAMPBELL (**3**); but without the younger stages of *S. simplex* and more of the young stages of *N. advena* (?) it is impossible to say whether this resemblance is more than superficial. From the large end of this conical embryo a cotyledonary ridge is now produced which extends almost entirely around this end and almost completely encloses the plumule (*fig. 17*), while in *N. advena* of the north it extends only a little more than half the distance around the embryo. This monocotyledonous character is very evident in embryos dissected out of the sacs. Two cotyledonary lobes are next developed from this cotyledonary ridge, thus giving it the dicotyledonous character (*fig. 18*). The development of this dicotyledonous character is much earlier and much more pronounced than in *N. advena* of the north. A number of embryos were cross sectioned and examined very carefully and considerable variation was found in the prominence of this character. In one case it was so great as to give the appearance of two equal cotyledons (*fig. 19*). The development is strikingly similar to that of Nelumbo as described by LYON (**18**) and YORK (**28**).

SCHAFFNER (**26**) dissected the advanced embryos of *N. advena* out of the sacs and clearly demonstrated the formation of the two cotyledonary lobes. He did not contradict my conclusions, as stated by MOTTIER (**20**), but made his studies from older embryos than I was able to secure at the time my studies were made.

The embryos of the two species of Castalia show some differences and also differ from *Castalia odorata*. In *Castalia ampla* a proembryo is formed which may consist of as many as six cells in linear arrangement (*figs. 20, 21*). The terminal cell then divides by a longitudinal wall, which is followed by a similar division in the next cell (*fig. 21*). The four cells thus formed then divide by a second longitudinal wall at right angles to the first. By repeated division, this mass of cells now forms a spherical embryo supported by a suspensor of four or five cells in linear arrangement (*fig. 22*). One or more of these suspensor cells, usually the basal, may divide longitudinally. On account of the seed pods sinking soon after fertilization it was impossible to follow the development in this species further.

In *Castalia pubescens* the embryo develops in the same manner, except that there are usually not more than four cells in the proembryo. With the formation of the spherical embryo the suspensor increases in diameter and the cells usually divide longitudinally (*figs. 24, 25, 26*). After the spherical stage the embryo gradually assumes a pear-shape, and a little later develops the collar-like ridge which extends about two-thirds around the embryo at its greatest circumference. This condition was readily demonstrated by two series of longitudinal sections cut at right angles to each other and a series of cross sections (*figs. 27–30*). *Fig. 27* is from a longitudinal section passing through the middle (x) and between the two points of the crescent-shaped cotyledonary ridge (y). *Fig. 28* is from a longitudinal section at right angles to *fig. 27* and passes through the cotyledonary ridge near the points of the crescent (z). *Fig. 29* is from a series of cross sections of an embryo of corresponding age to *figs. 27* and *28*. *Fig. 30* is from section *d* of *fig. 29*, i. e. at about the point where the cotyledonary ridge arises. *Fig. 31* is reconstructed from a series of sections of a slightly older embryo. At this time there was no external indication of the two cotyledonary lobes, but the rapid division of cells just within the points of the crescent-shaped cotyledonary ridge (*fig. 30c, 1*) indicates their early formation.

It was impossible to follow the development of the embryo beyond this point, because of the withdrawal of the seed pods from the surface of the water to the bottom, where they were quickly buried in the mud. This withdrawal commenced soon after pollination and was accomplished by the spiral-like formation of the peduncle which gradually contracts. However, SCHAFFNER (**26**) was able to dissect the young embryos of *Castalia odorata* out of their sacs and makes the following statement concerning them:

> Although the "dicotyl" appearance is quite strong, the embryo must be regarded as the same type as Nymphaea and Nelumbo. In the very young embryo there is an expansion which extends nearly around the base but is discontinuous at one side. Soon this expansion develops on opposite sides as two prominent lobes in such a manner that the original connection between the two lobes is very difficult to distinguish. On examining the embryo from below, however, similarity to the Nelumbo and Nymphaea embryos becomes perfectly apparent. There is the same opening on one side, and on the back a connection of the two lobes, only to a less extent. Unless special care were taken in recon-

structing such an embryo from serial sections, one might readily take it for a dicotyl. It will be evident, however, from a comparison of the figures that the Castalia embryo represents only the extreme of the lobing shown in Nelumbo and Nymphaea.

The formation of the suspensor is entirely different from what I observed in *C. odorata*, but corresponds with CONARD'S (**5**, **6**) observations. The suspensor disappears soon after the formation of the cotyledonary ridge.

The development of the embryos of *Brasenia purpurea* and *Cabomba piauhiensis* is practically the same, but since *C. piauhiensis* is much more easily sectioned and furnished much better preparations, most of the drawings were made from it. The fertilized egg divides by the formation of cross walls and produces a proembryo of three or four cells in linear arrangement (*figs. 32, 33a, 34, 35*). The terminal cell then divides, forming a quadrant (*fig. 33a*), then it forms the octant, and then a large spherical embryo supported by a short suspensor of two or three cells which usually divide longitudinally (*figs. 34, 35, 36*). As the embryo increases in size, it becomes more or less flattened against the walls of the sac and develops the cotyledonary ridge (*fig. 36, x*) similar to the two genera just described, except that this ridge extends almost entirely around the plumule, thus forming a pit with the plumule in the center. The dicotyledonous character produced by the development of the cotyledonary lobes appears very early. Only by the most careful examination of the intermediate stages at the time of the first appearance of the cotyledons, and by the most careful cross sections was it possible to demonstrate the common origin of these two cotyledonary lobes. They develop very early and the edges and tips come together, thus enclosing the plumule in a short, hollow cone (*fig. 37*). After this the development of the embryo is a mere increase in size (*figs. 38, 39*), accompanied by the modification of the endosperm previously referred to. The suspensor persists until the embryo is almost mature and then disintegrates.

It will be noted that the young embryo of *Nymphaea advena* (?) is similar to the embryos of *Lysichiton kamtschatense* as described by CAMPBELL (**2**); and of *Ceratophyllum submersum* as described by STRASBURGER (**23**). The young embryos of *Castalia ampla*, *C.*

pubescens, *Brasenia purpurea*, and *Cabomba piauhiensis* all have the same general character as *Nymphaea advena*, except that they possess suspensors. They also show some resemblance (which may be superficial) to the embryo of *Sparganium simplex* as described by CAMPBELL (**3**). They also resemble the embryos of *Naias flexilis* and *Zannichella palustris* as described by CAMPBELL (**1**), *Potamogeton foliosus* and *P. natans* as described by WIEGAND (**27**) and HOLFERTY (**10**), and *Limnocharis emarginata* as described by HALL (**9**) except that they do not possess the large basal cell of the suspensor. The late development of the suspensor in *Nymphaea advena* (?) of Cuba and *N. advena* of the north, as previously described by me, may confirm in some measure COULTER and CHAMBERLAIN'S view that the Alisma-type of monocotyledonous embryo is primitive and that the suspensor in the Pistia type has been suppressed.

It will also be noted that the origin of the cotyledonary lobes in all cases is from a crescent-shaped cotyledonary ridge about the larger part of the embryo, and that my results coincide with the conclusions reached by LYON, SCHAFFNER, and YORK. This point in CONARD'S studies is illustrated by a single figure (*48, d*) of *Castalia caerulea*. This figure agrees exactly with *fig. 30* and text *fig. 2, d, e* of my first paper, with LYON'S *fig. 10*, and YORK'S *fig. 33* of Nelumbo. However, my figures are parts of series which illustrate the true monocotyledonous character of the embryo; and this monocotyledonous character of *C. odorata* was afterwards demonstrated by SCHAFFNER who dissected the embryos out of their sacs.

RICHARD (**21**) referred to the embryos of the grasses, Nelumbo, Ruppia, Hydrocharis, and Zostera as *embryons macropodes*, and SCHAFFNER (**26**) confirms this view and expresses the opinion that the massive expansion and lobes of Halophila, Ruppia, Zostera, Nelumbo, Nymphaea, and Castalia are not homologous with the cotyledons, but are specially developed absorbing organs.

The figures of this paper show a striking resemblance to the figures of anomalous dicotyledons by LEWIS (**16**) and MOTTIER (**20**). However, the flowers show more monocotyledonous than dicotyledonous characters, while only the leaves may be considered as uniformly presenting dicotyledonous characters. It appears, therefore, that the Nymphaeaceae can be more properly classed as anomalous monocotyledons, rather than as anomalous dicotyledons as suggested by MOTTIER.

SUMMARY.

1. The development of the embryo sac is practically the same in all species.

2. In all species the endosperm nucleus divides and the daughter nucleus in the antipodal end enters a nucellar tube or sac which penetrates the nucellus.

3. This nucellar tube or sac is apparently for the purpose of transferring food from the nucellus to the endosperm, from which it is transferred to the embryo.

4. The endosperm is of two types: the cellular in Nymphaea and Castalia, and the nuclear followed by the cellular in *Brasenia purpurea* and *Cabomba piauhiensis.*

5. The character of the endosperm in the late stages of *Brasenia purpurea* and *Cabomba piauhiensis* indicates a greater importance in germination than in the other genera.

6. The embryo of *Nymphaea advena*(?) originates as a spherical mass of cells and later develops a cotyledonary ridge and suspensor, while the other species develop embryos consisting of a single row of cells, from which is formed a spherical embryo supported by a suspensor. A crescent-shaped cotyledonary ridge is then developed, ranging from two-thirds to almost the entire distance around the embryos.

7. With the development of the cotyledonary ridge, two cotyledonary lobes are produced which may readily be mistaken for two cotyledons.

ESTACIÓN CENTRAL AGRONOMICA,
Santiago de las Vegas, Cuba.

NOTE: The material from which these studies were made was submitted to specialists in taxonomy. There was some difference of opinion as to whether the Nymphaea was a large-leaved form of *N. advena* or another closely related species. *Castalia pubescens* is an introduced species from eastern India, Philippines, Java, and Australia. It was collected in a large lagoon near San Antonio de las Baños in Havana Province. *Nymphaea advena*(?) was collected in the river at San Cristobal and in a small lagoon south of Herredura in Pinar del Rio Province; all other species in this same small lagoon. Specimens of all these species have been deposited in the New York Botanical Garden.

LITERATURE CITED.

1. Campbell, D. H., A morphological study of Naias and Zannichellia. Proc. Calif. Acad. Sci. III. **1**:1–62. *pls. 1–5.* 1897.
2. ——— Notes on the structure of the embryo sac in Sparganium and Lysichiton. Bot. Gazette **27**:153–166. *pl. 26.* 1899.
3. ——— Studies on the flower and embryo of Sparganium. Proc. Calif. Acad. Sci. III. **1**:293–328. *pls. 46–48.* 1897.
4. ——— On the affinities of certain anomalous dicoyledons. Amer. Nat. **36**:7–12. *figs. 2.* 1902.
5. Conard, H. S., Note on the embryo of Nymphaea. Science N. S. **15**:316. 1902.
6. ——— The water lilies: a monograph of the genus Nymphaea. The Carnegie Institution of Washington, Publication No. 4. 1905.
7 Cook, Mel. T., Development of the embryo sac and embryos of *Castalia odorata* and *Nymphaea advena.* Bull. Torr. Bot. Club **29**:211–220. *pls. 12–13.* 1902.
8. Coulter, J. M., and Chamberlain, C. J., Morphology of angiosperms. 1903.
9. Hali, J. G., An embryological study of *Limnocharis emarginata.* Bot. Gazette **33**:214–219. *pl. 9.* 1902.
10. Holferty, G. M., Ovules and embryo of *Potamogeton natans.* Bot. Gazette **31**:339–346. *pls. 2–3.* 1901.
11. Ikeda, T., Studies in the physiological functions of the antipodals and related phenomena of fertilization in Liliaceae. I. *Trycirtis hirta.* Coll. Agric. Imp. Univ. Tokyo **5**:41–72. *pls. 3–6.* 1902.
12. Johnson, D. S., On the development of *Saururus cernuus.* Bull. Torr. Bot. Club **27**:365–372. *pl. 23.* 1900.
13. ——— On the endosperm and embryo of *Peperomia pellucida.* Bot. Gazette **30**:1–11. *pl. 1.* 1900.
14. ——— On the development of certain Piperaceae. Bot. Gazette **34**:321–340. *pls. 9–10.* 1902.
15. ——— Seed development in the Piperaceae and its bearing on the order. Johns Hopkins Univ. Circ. **178**:29–32. 1905.
16. Lewis, C. E., Studies on some anomalous dicotyledonous plants. Bot. Gazette **37**:127–138. *pls. 7–8.* 1904.
17. Lyon, H. L., Preliminary note on the embryogeny of Nelumbo. Science N. S. **13**:470. 1901.
18 ——— Observations on the embryogeny of Nelumbo. Minn. Bot. Studies **2**:643–655. *pls. 48–50.* 1901.
19. ——— The embryo of the angiosperms. Amer. Nat. **39**:13–34. *figs. 11.* 1905.
20. Mottier, D. M., The embryology of some anomalous dicotyledons. Annals of Botany **19**:447–463. *pls. 26–27.* 1905.

21. RICHARD, L. C., Analyse botanique des embryons endorhizes ou monocotyledonés, et particulièrement de celui des Graminées. Annales Paris Mus. Nat. Hist. **17**:223–251, 442–487. 1811.

22. SARGENT, ETHEL, Evolution of the monocotyledons. BOT. GAZETTE **37**: 325–345. *figs. 6.* 1904.

23. STRASBURGER, E., Ein Beitrag zur Kenntniss von *Ceratophyllum submersum* und philogenetische Erörterungen. Jahrb. Wiss. Bot. **37**:477–526. *pls. 9–11.* 1902.

24. SCHAFFNER, J. H., The embryo sac of *Alisma Plantago.* BOT. GAZETTE **21**:123–132. *pls. 9–10.* 1896.

25. ——— The life history of *Sagittaria variabilis.* BOT. GAZETTE **23**:252–273. *pls. 20–26.* 1897.

26. ——— Some morphological peculiarities of the Nymphaeaceae and Helobiae. Ohio Nat. **4**:83–92. *pls. 5–7.* 1904.

27. WIEGAND, K. M., The development of the embryo sac in some monocotyledonous plants. BOT. GAZETTE **30**:25–47. *pls. 6–7.* 1900.

28. YORK, H. H., The embryo sac and embryo of Nelumbo. Ohio Nat. **4**:167–176. 1904.

EXPLANATION OF PLATES XVI–XVIII.

Figures of the same relative value are drawn with the same lenses: *figs. 1–7* with Zeiss no. 4 oc. and $\frac{1}{12}$ obj.; *figs. 12–16, 20–28, 30, 32, 36,* and *40* with no. 4 oc. and DD obj.; *figs. 8–11, 17–19, 29, 31, 37–39* with no. 4 oc. and A obj.

PLATE XVI

FIG. 1. Archesporial cell of *Brasenia purpurea.*

FIG. 2. Megaspores of *Nymphaea advena* (?).

FIG. 2. Uninucleate embryo sac of *N. advena* (?).

FIG. 4. Mature embryo sac of *Castalia pubescens*, showing entrance of pollen tube (*pt*).

FIG. 5. Embryo sac of *C. pubescens* just after fertilization, showing fertilized egg (*o*), remains of synergids (*syn*), and the endosperm nucleus.

FIG. 6. Embryo sac of *Brasenia purpurea* just after fertilization, showing egg (*o*), synergid (*syn*), endosperm nucleus (*end nu*), and starch in the antipodal end of the sac.

FIG. 7. Embryo sac of *Cabomba piauhiensis*, showing fertilized egg (*o*), the two synergids (*syn*), the endosperm nucleus (*end nu*) after first division, and the remains of a second sac (*e s*).

FIG. 8. Embryo sac of *N. advena* (?), showing two-celled embryo, the nucellar tube, and the two daughter cells of the endosperm nucleus (*en*) separated by a wall; the tube is about three-fourths the length of the ovule.

FIG. 9*a*. Embryo sac of *C. pubescens*, showing large pear-shaped embryo with region of modified endosperm (*x*), and the nucellar tube.

FIG. 9*b*. Cross-section of nucellar tube of 9*a*.

FIG. 10. Embryo sac of *C. piauhiensis*, showing two-celled embryo and nucellar tube. The endosperm nucleus has divided and one daughter cell entered the tube (*ntn*), while the other has remained in the sac and undergone first division (*end*).

FIG. 11*a*. Embryo sac and mature nucellar tube of *C. piauhiensis* with spherical embryo; the thin endosperm filled the sac at this time.

FIG. 11*b*. Cross-section of tube of *11a* at smallest part.

FIGS. 12–19. *Nymphaea advena*(?).

FIG. 12*a*. Two-celled embryo with daughter nucleus of endosperm nucleus (*en*) after first division; same as *fig. 8*.

FIG. 12*b*. Nucellar tube nucleus of *figs. 8* and *12a*.

PLATE XVII

FIG. 13*a*. Section of spherical embryo in octant stage surrounded by endosperm.

FIG. 13*b*. Lower part of the nucellar tube of *13a* in which the nucellar tube nucleus was divided.

FIG. 14. Mature nucellar tube nucleus.

FIG. 15. Spherical embryo.

FIG. 16. Pear-shaped embryo at time of origin of cotyledonary ridge and with well-developed suspensor.

FIG. 17. Cross-section of embryo a little older than that in *fig 16*.

FIG. 18. Cross-section of embryo older than that in *fig. 17*, showing monocot character in lower part and dicot character in upper part; 3d, 4th, 6th, 14th, 19th, and 24th sections.

FIG. 19. Cross-section of embryo showing equal cotyledonary lobes (dicot characters); 1st, 4th, 5th, 7th, 8th, and 15th sections.

FIGS. 20–22. *Castalia ampla*.

FIG. 20. Embryo sac and two-celled embryo showing endosperm and nucellar tube nucleus (*ntn*) in sac-like nucellar tube.

FIG. 21. Older stage of same, showing absorption of nucellar tube and nucleus (*ntn*) by endosperm.

FIG. 22. Spherical embryo with suspensor.

PLATE XVIII

FIGS. 23–31. *Castalia pubescens*.

FIG. 23. Two-celled embryo and endosperm; the endosperm has penetrated the upper part of the nucellar tube.

FIG. 24. Spherical embryo with suspensor and endosperm, also showing elongated nucellus cells in axis of ovule below sac (*enc*).

FIG. 25. Older stages of the same showing enlargement of sac at right angles to the original long axis.

FIG. 26. Young pear-shaped embryo.

FIG. 27. Longitudinal section of embryo passing through middle of crescent-shaped cotyledonary ridge (*x*) and between the points of the same (*y*).

FIG. 28. Longitudinal section at right angles to *fig. 27* passing through the cotyledonary ridge (*zz*) near the points of the crescent.

FIG. 29. Cross sections of embryo at about same age as *figs. 27* and *28*.

FIG. 30. Section *d* of *fig. 29; cl*, cotyledonary lobes; other letters same as in *figs. 27* and *28*.

FIG. 31. Reconstruction from sections of embryo a little older than those in *figs. 27–30*.

FIGS. 32–40. *Cabomba piauhiensis.*

FIG. 32. Two-celled embryo.

FIG. 33*a*. Section of embryo in octant stage showing two-celled suspensor.

FIG. 33*b*. Endosperm of 33*a*.

FIG. 34. Spherical embryo with three-celled suspensor.

FIG. 35. Spherical embryo showing original two-celled suspensor subdivided by longitudinal divisions.

FIG. 36. Longitudinal section of embryo at about time of origin of cotyledonary ridge, showing two-celled suspensor; cut same direction and showing same points as *fig. 27*.

FIG. 37. Reconstruction from section of embryo slightly older than *fig. 36* and showing early development of cotyledonary lobes.

FIG. 38. Reconstruction from sections of almost mature embryo; drawn to same scale as *fig. 37*.

FIG. 39. Cross-sections of embryo; 2d, 6th, 8th, 12th, 24th, and 28th sections.

FIG. 40. Endosperm from embryo near same age or little older than *fig. 38*.

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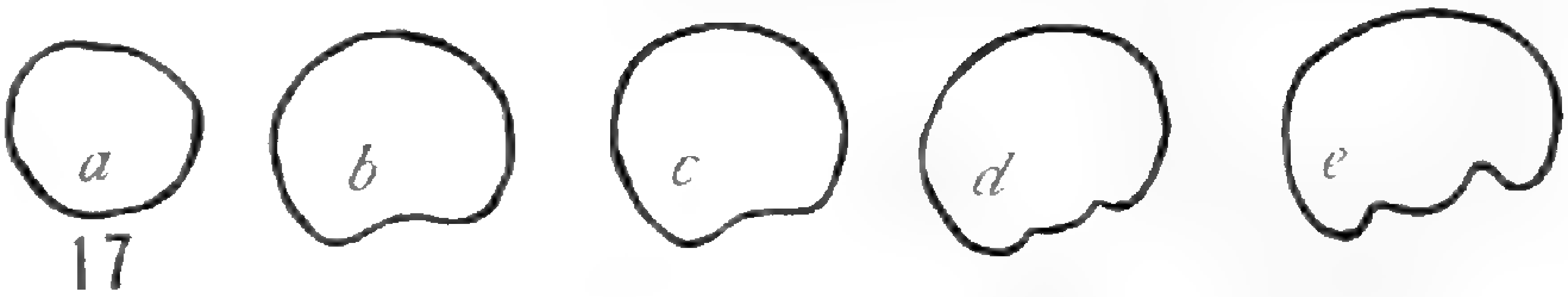
13*b*



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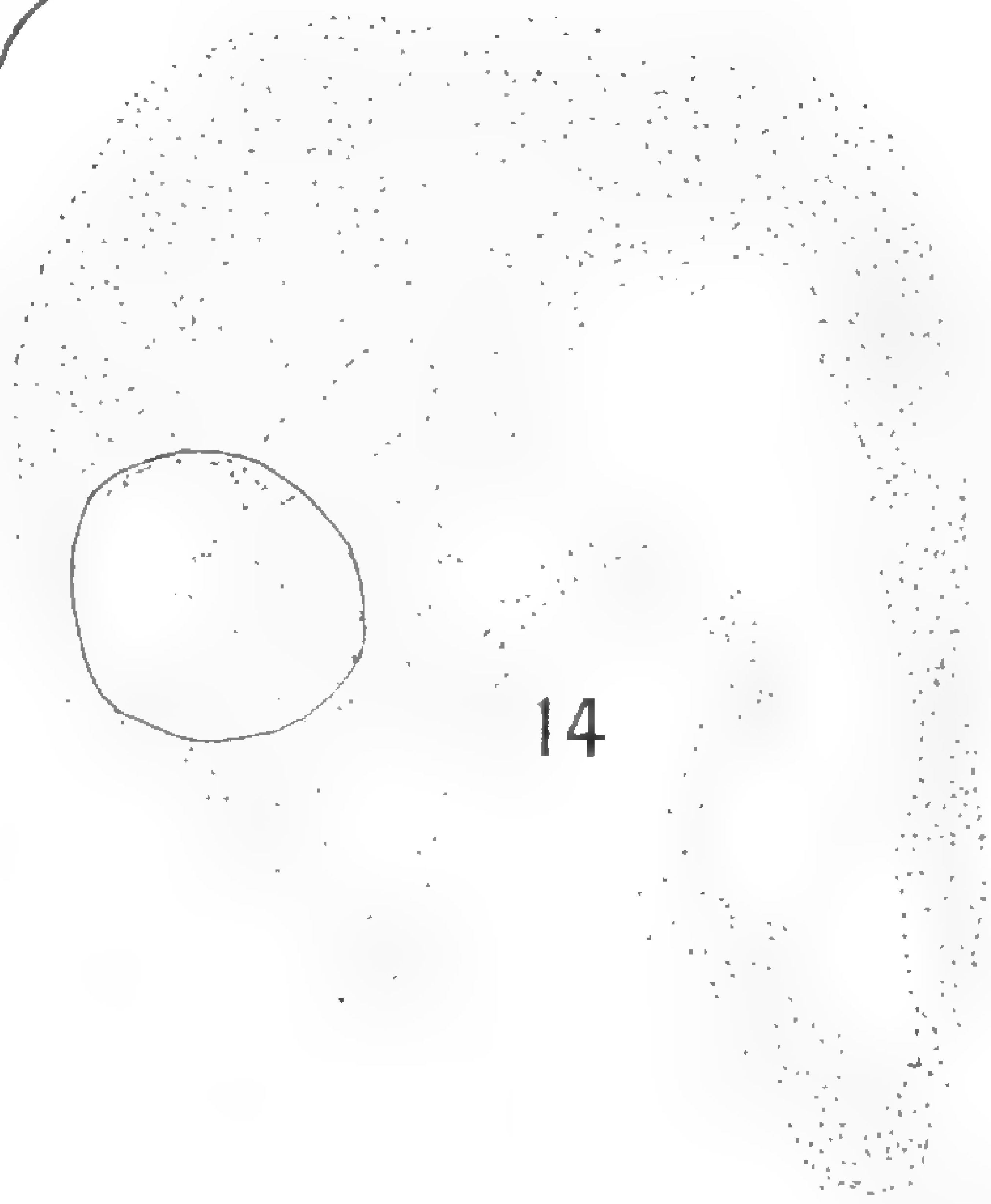
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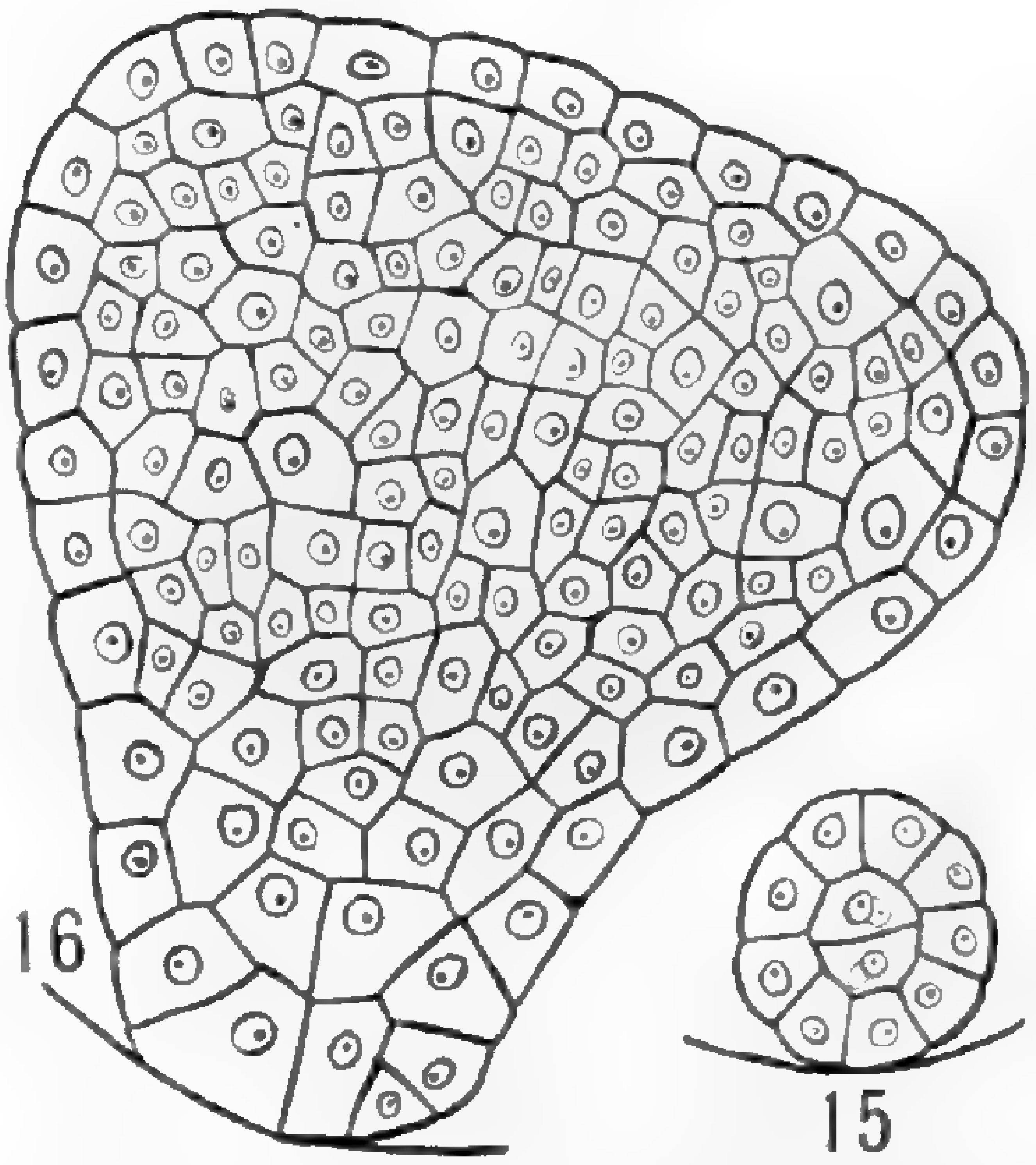
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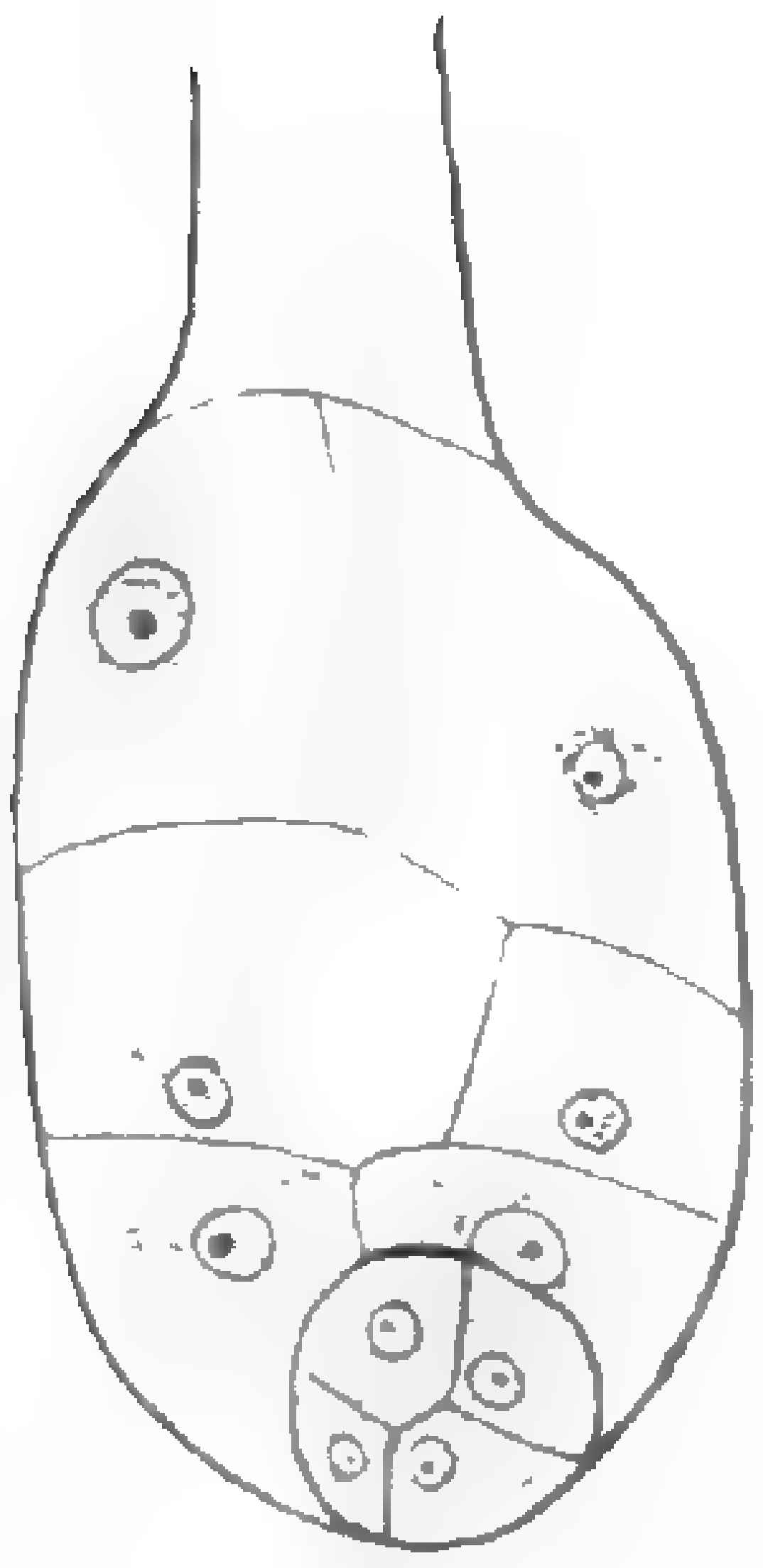
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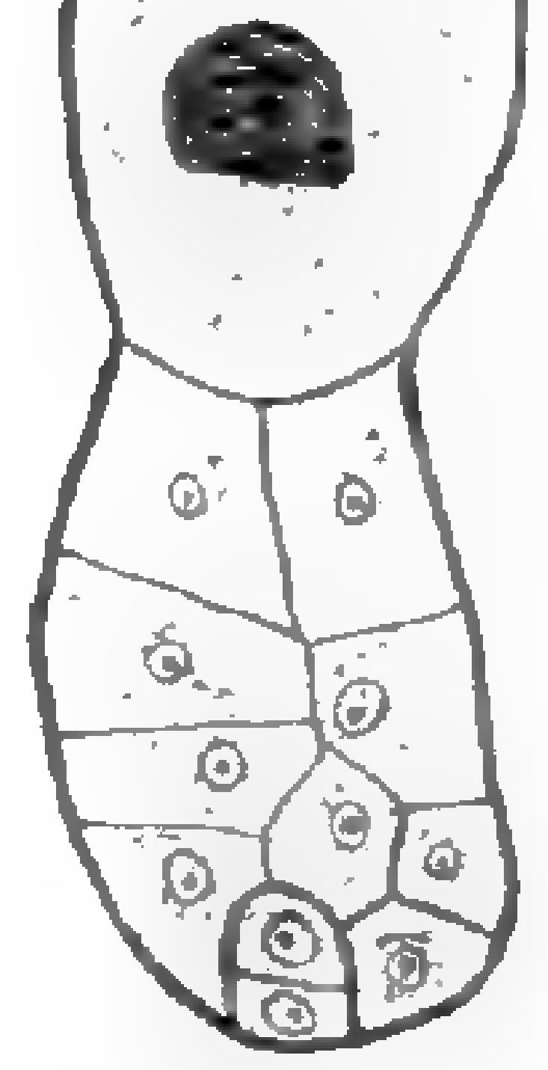

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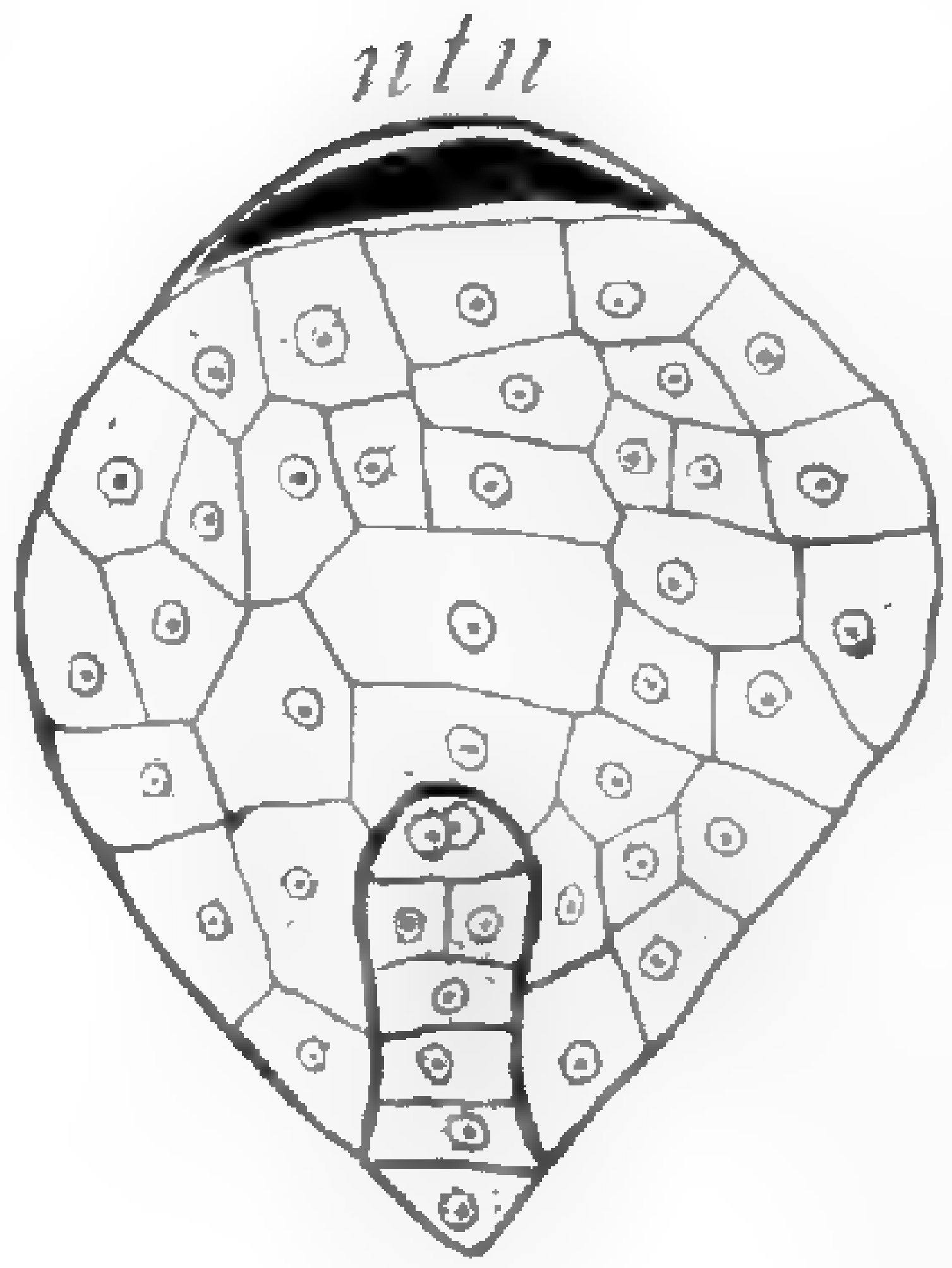

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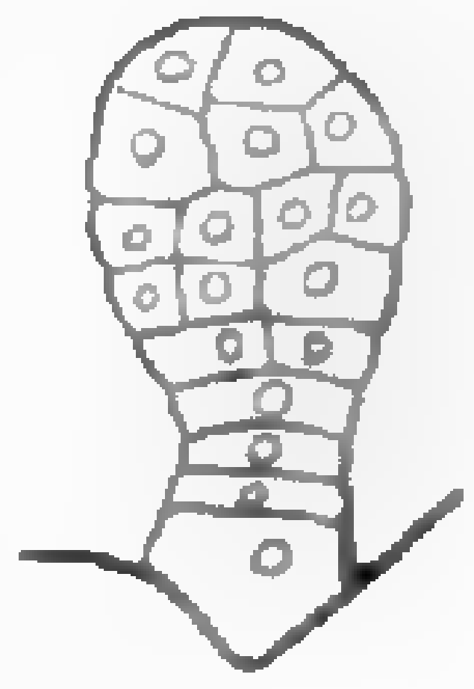
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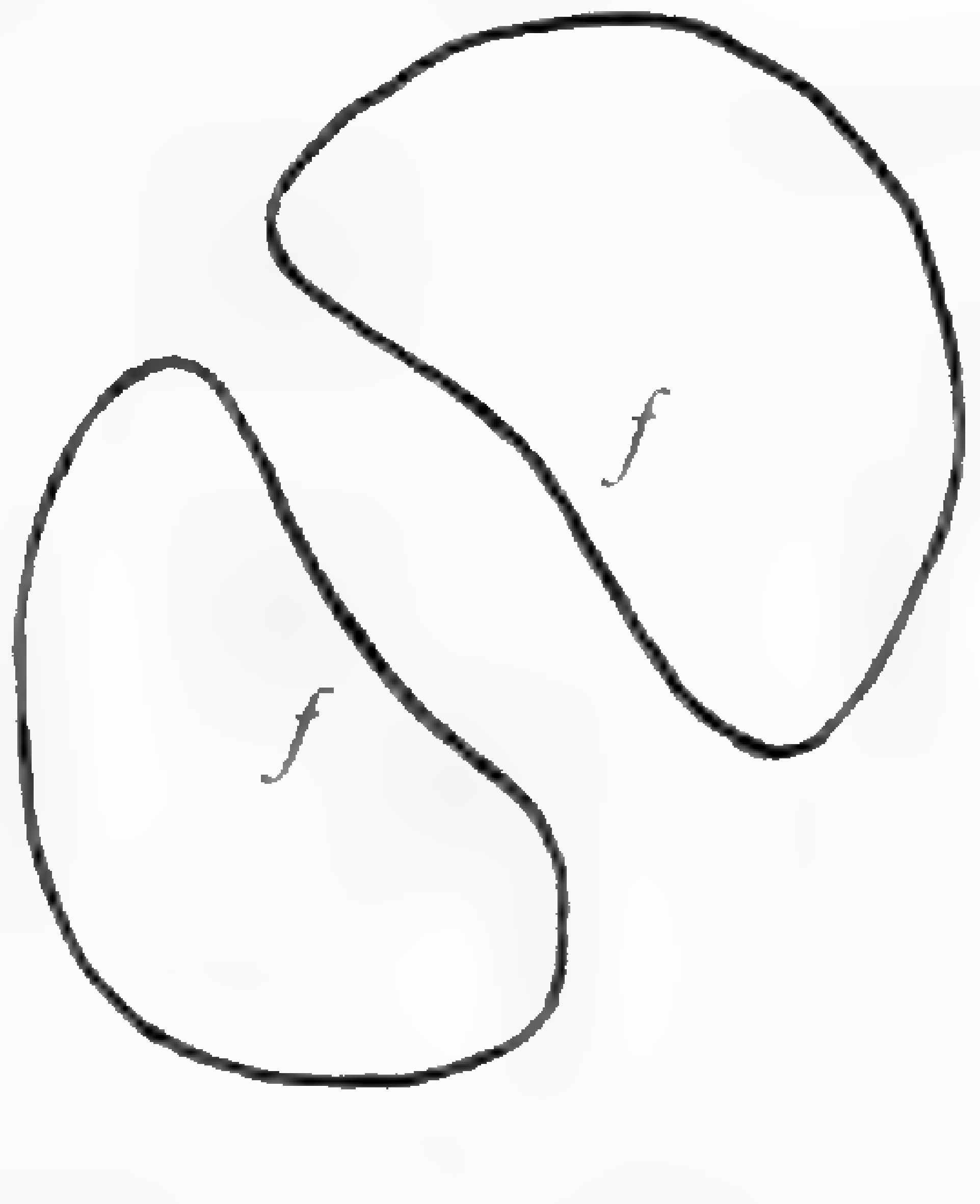

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BOOK REVIEWS.

Two new western "Floras."

DR. RYDBERG has long been at work on a flora of the Rocky Mountain region, and in connection with his studies there have been many new species added and much critical work published. Therefore, when the Agricultural Experiment Station of Colorado was compelled to complete the determinations of its collections, it was natural to turn to DR. RYDBERG, and the result is a station bulletin dealing with the flora of Colorado.[1] As was to be expected, the work grew in the preparation, so that it is nearly an exhaustive list of the plants at present known in Colorado. It is not a full descriptive manual in the ordinary sense, for under the species one finds only synonymy, range, and stations; but the analytical keys should enable one to determine the genus and species of all the forms ordinarily met. In this way 2,912 species of vascular plants are characterized, and this number is said to be surpassed by no state except California and perhaps Florida. It is quite characteristic of this great flora that one-fifth of it belongs to the Compositae, and that there are only twenty gymnosperms and forty pteridophytes. The nomenclature used by the author is well known, as are also his views on generic limitations. As he himself says in the introduction, he "belongs to that radical school which believes in small genera with closely related species, rather than in larger ones with a heterogeneous mass of different groups of plants having relatively little relationship to each other." The author also says that "the nomenclature used is in principle agreeing with the so-called American code adopted at a meeting in Philadelphia, and submitted to the International Botanical Congress at Vienna, with a few modifications resulting from a compromise with the European botanists." If this means that the Vienna Code is used only in so far as it meets the approval of the individual, then international congresses on nomenclature will be of little value until they achieve the impossible result of formulating a code that will satisfy all taxonomists. Very wisely the author publishes in this bulletin no new genera or species, or even new names or combinations. This publication will certainly serve a most useful purpose, and both author and station are to be commended for carrying it through.

The other flora is that of Washington by CHARLES V. PIPER[2]. The author says that his "principal aim is to present a summary of our present knowledge

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[1] RYDBERG, P. A., Flora of Colorado. Agric. Exp. Sta. Colorado, Bull. 100. pp. xxii+414. 1906.

[2] PIPER, CHARLES V., Flora of the State of Washington. Contrib. U. S. Nat. Herb. **11**:1–637. *pls. 1–22* and colored map. 1906.

of the vascular plants of Washington and to call attention to the more important problems, both taxonomic and ecological, which have become disclosed." The plan of the work is practically that of Dr. RYDBERG'S, namely a list of species with synonymy, range, etc., but with simple keys for general identification. The views as to the limitations of genera and species, however, are much more conservative, the author making the following interesting remarks: "It is at least doubtful if the very large number of new names thus occasioned does not more than counterbalance any advantage argued in favor of the practice. Certainly the carrying of the practice to such an extreme that genera are considered to be made up of species of similar habit, rather than to be based on structural character, seems inadvisable. Neither does it impress one as a valid argument that, because in some extremely natural families the genera must perforce be based on very slight differences, similar characters must be given equal consideration in all families." The pages given to an account of the botanical explorers of Washington, beginning with MENZIES, are most interesting, as is also the account of the physiographic features of the flora. The "annotated catalogue" comprises a very long list of vascular plants, and it is interesting to note that 185 of them are endemic, two of the genera included in the list (Rainiera and Hesperogenia) being monotypic. The number of gymnosperms is almost exactly that given above for Colorado, but the pteridophytes are more numerous, a list of 64 being given.—J. M. C.

AN INTRODUCTION to plant physiology by the LINSBAUERS[3] is very welcome and it is to be hoped that an English edition will be prepared. While too elaborate for our secondary schools at present, and yet too elementary for higher students, the work contains a great deal that may be efficiently adapted to any first course. The diction is semipopular. The first commendable feature one notes is the logical arrangement of the topics. The experiments (nearly 300) accompany the text, in fact are really a part of it. Following each chapter is a series of problems for independent investigation, so that each chapter first equips the student for independent work and then suggests that he do some as indicated. The difficult topics of semipermeability, osmosis, etc., are skilfully approached by preliminary experimentation with imbibition phenomena. Physical explanations involving such difficult subjects as solution-tension are very properly omitted. The treatment of some processes is far from modern. The combustion conception of respiration is developed. Photosynthesis is called "assimilation" and contrasted with respiration, which is also given the name of "dissimilation." This is a very unfortunate confusion of both terms and ideas. Of the seventy-eight cuts of the text proper, seven illustrate apparatus original in design.—RAYMOND H. POND.

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[3] LINSBAUER, LUDWIG, und LINSBAUER, Karl, Borschule der Pflanzenhpysiologie. Eine experimentale Einführung in das Leben der Pflanzen. 8vo. pp.— *figs. 78.* Carl Konegen, Vienna. 1906.

MINOR NOTICES.

Pflanzenfamilien.[4]—Part 226 contains the completion of the Neckeraceae and the beginning of the Lembophylaceae by V. F. BROTHERUS. The second part of the second supplement has also appeared, including the literature of 1899–1904 in reference to dicotyledons up to the beginning of Euphorbiaceae. —J. M. C.

NOTES FOR STUDENTS.

Archegoniatenstudien.—The tenth of GOEBEL's series by this title is for size almost a book in itself. It is made up of over twenty papers on morphology and biology of mosses and liverworts, varying from a page or less, embodying a brief note on the water adaptation in the form and position of the leaves in Orthorhynchium, to a paper of forty-odd pages on Dawsonia and its allies, and a like one on marsupiferous Jungermanniales. In great part these papers were written several years ago, and some of the researches have been epitomized in GOEBEL's *Organographie*, but they have not been published *in extenso* until now, on account of other work.

Together they form a most important contribution to our knowledge of the bryophytes—a contribution too full of details to report fully. At various places it has a tinge of the polemic, for the author has to clear away many errors, and he takes occasion to rebuke one and another for shortcomings. Much space is devoted to speculations, which are confessedly unsupported by investigation because material or time was lacking. Such speculations, if put briefly, may be suggestive as a guide to future investigations; but they appear to be indulged in as a basis for future claims to priority, if we may judge from some citations of earlier ones in these pages. Even a scientific man is rarely without a prejudice in favor of his own hypotheses. Thus the author guessed (*Organographie* 346) about the development of the multicellular "spores" of Dicnemon: "Am wahrscheinlichsten ist es dass sich aus den gekeimten Sporen ein Fadenprotonema bildet, etwa aus den Brutknospen von Tetraphis." Now he declares "dass die früher geäusserte Vermutung richtig war." But the "protonemal filaments" function "der Hauptsache nach als Rhizoiden;" rhizoids arise also from the surface; and the apical cell of the stem arises not as a branch of one of these "protonemal filaments" but almost immediately from a marginal cell of the "spore." It is difficult to see how the earlier guess can possibly be justified by these observations. Certainly the resemblance to the behavior of the gemmae of Tetraphis is rather remote. Other like instances might be cited; sometimes the guess was right, sometimes not; and that is likely to be the case with these new ones. But the observations are abundant, and the author's keen discrimination and clear presentation throw light upon many obscure points.

Dawsonia is held to be the primitive form of the Polytrichum line by reason of the limited differentiation of tissues in the axis of the gametophyte, and espe-

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[4] ENGLER, A., und PRANTL, K., Die natürlichen Pflanzenfamilien. Lieferung 226. Leipzig: Wilhelm Engelmann. 1906.

cially on account of the structure of the peristome, whose development and anatomy he clears up. He also points out the relations of the peristome of the Buxbaumiaceae and Tetraphideae to that of the Polytrichaceae.

Dicnemonaceae (Dicnemon and Mesotus) are recognized as a natural group, characterized by the multicellular spores and the peculiar filamentous outgrowths on the leaves. which are considered as organs of water absorption. Both these characters and the structure of the sporophyte indicate adaptation for alternating dry and wet periods.

Leptostomum has a peristome corresponding to a degenerate mniaceous peristome. In Eriopus a fuller description is given of the leaves and of the rhizoids at the base of the sporophyte than in *Organographie* 377.

The symmetry of the leaves and their position on the axis is discussed at some length for the genera Pterygophyllum, Cyathophorum, Mittenia, Rhizogonium, and Orthorhynchium, and there are minor notes on sundry points.

The development of the leaves of several species of Gottschea is shown to be of the same type as in Fissidens; multicellular rhizoids are described and figured; the absence of a perigone is correlated with the boring of the embryo sporophyte deep into the stem; and *G. splachnophylla* shows a basal elaterophore like that of Pellia.

Paraphyllia were found in five genera, functioning in part for photosynthesis and in part for holding water.

The "Geocalyceae" are described at length, and for them the more appropriate designation marsupiferous Jungermanniales is suggested. Three types are discriminated: (*a*) Tylimanthus type (Tylimanthus, Marsupellopsis, Marsupidium), with pouch originally solid and hollowed out by the growing embryo; (*b*) Isotachis type, in which the archegonium after fertilization is surrounded by a ring-like wall arising from the stem tissues, which carries up the leaves; (*c*) the common type, with pouch arising after fertilization, hollow from the beginning (Balantiopsis, Acrobolbus, Lethocolea) There are intermediate forms between (*a*) and (*c*). In Acrobolbus there is even a "root-cap" on the pouch.

Another heterophyllous Radula, *R. uvifera*, is described, the so-called "slender male spikes" of hepaticologists being here, as in *R. pycnolejeunioides*, composed of small water sacs, frequently inhabited by animalcules; whereas the antheridia are protected by quite different leaves. Hymenophyllum, with its slender "stalk" and broader "leaf" shows no constancy in this differentiation, and since Pellia, Preissia, Fegatella, etc., show similar forms on being grown in the dark and then illuminated, the author is moved to conclude that "the stalk arises . . . . by autonomous etiolation"—a charming phrase which we owe to SACHS, but nevertheless a phrase which is merely a wordy cloak for ignorance.

The rudimentary "leaves" of *Blyttia xiphioides* are organs of protection for the apical region. The remarkable but inconstant water sacs of *Metzgeria saccata* arise, it is said, not by a lobing of the thallus, but by "an inrolling of the thallus margins from below and locally accelerated growth of isolated parts"—which latter sounds much like lobing in other words.

The liverworts furnish most instructive examples of parallel structures, of which the author cites many instances.—C. R. B.

Anaerobic respiration.—Inasmuch as PALLADIN and KOSTYTSCHEW, working independently, had agreed, contrary to the conclusions of several other observers, that anaerobic respiration was not identical with alcoholic fermentation, it seemed good to them to reinvestigate the question. They now find[5] that while not identical in all plants and under all conditions, there are striking coincidences. For example, in living lupine seeds and seedlings they consider the anaerobic respiration identical with alcoholic fermentation; but in frozen lupine seedlings and stem tips of *Vicia Faba* the former has nothing to do with the latter. In pea seeds and wheat embryos, living and frozen, there occurs a considerable formation of alcohol, and the anaerobic respiration is "in great part" alcoholic fermentation. They confirm the results of GODLEWSKI, STOCKLASA, and others regarding the presence of "zymase," but think it yet remains to be shown that it is identical with yeast zymase. Under certain conditions aceton and its allies are formed, both in aerobic and anaerobic respiration of living and frozen plants.

It becomes more and more evident that the course of the respiratory decomposition of the protoplasm may be varied.—C. R. B.

Thermal death-point.—MEYER[6] has determined a formula by which may be calculated the time necessary to kill bacteria at any given temperature, when observation has determined the time necessary at any two convenient temperatures, such as 80° and 100°. This rests upon the observation that the death periods form a geometrical progression, decreasing with the increasing temperatures. Thus the formula is $q=\sqrt[n-1]{\frac{a}{t}}$, in which a is the first member of the progression, t any other known member, q the progression, n the number of terms. Thus, BLAU had determined the death period of *Bacillus subtilis* at 100° as 180 minutes, and at 80° as 4500 minutes. Whence $q=\sqrt[2]{\frac{180}{4500}}=0.2$. The calculated series then would be: 80°, 4500 minutes; 90°, 900 minutes; 100°, 180 minutes; 110°, 36 minutes; 120°, 7.2 minutes; 130°, 1.4 minutes; 140°, 0.28 minutes or 17 seconds; 150°, 3.4 seconds. The figures observed by MEYER agree well with these calculations. In practice this has an important application in enabling one to calculate the supramaximal temperature, as ENGELMANN called it, i. e., the time necessary to kill any form instantly—say in one second.—C. R. B.

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[5] PALLADIN, W., and KOSTYTSCHEW, S., Anaerobe Atmung, Alkoholgärung und Acetonbildung bei den Samenpflanzen. Ber. Deutsch. Bot. Gessels. **24**:273–285. 1906.

[6] MEYER, ARTHUR, Notiz über eine die supramaximalen Tötungszeiten betreffende Gesetzmassigkeit. Ber. Deutsch. Bot. Gesells. **24**:340–52. 1906.

Geotropic stimulation and position.—CZAPEK[7] has replied to FITTING with a paper which is largely a comparative study of the methods and results of the workers in this problem. The author concedes to FITTING that in many cases stronger stimulation occurs at 90° than at 135°. On the other hand, FITTING'S conclusion that 45° above the horizontal and 45° below are equivalent positions is rejected. The reaction time is found to be practically the same at deviations between 20° and 160°, but is noticeably longer either above or below those limits. The method of anti-ferment reaction shows that the stimulation is clearly less at 45° below than at 45° above. In the inverse position there is no anti-ferment reaction. Just how much significance is to be attributed to the results of this method the reviewer cannot say. CZAPEK believes that in spite of all the investigation of this problem a satisfactory solution is still in the future.—RAYMOND H. POND.

Chemistry of germination.—ZALESKI has studied certain changes that occur in the proteids of germinating seeds and contributes these points. The phosphorus-containing proteids and phosphatids (chiefly lecithin) are very quickly and almost totally decomposed by an enzyme, with the formation of "inorganic" phosphates, only 2 per cent. remaining unattacked. These bodies are apparently nucleo-albumins (phytovitellins). What the enzyme is, whether trypsin or a special one, remains to be investigated.[8] The formation of asparagin, like the proteid decomposition, is an enzymic process, proteolysis yielding material which forms asparagin in an unknown way and independent of temperature changes, at least in the later stages of germination. The nature of this process is to be further studied by the author.[9]—C. R. B.

Absorption of solutes by soils.—Bulletin 32 of the Bureau of Soils[10] is consistent with the high standard established by the previous publications of the Bureau. SCHREINER and FAILYER find as a general law in the case of phosphates that the amount of solute a given soil will withdraw from solution percolating through it is proportional to the quantity which the soil is still capable of absorbing.—RAYMOND H. POND.

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[7] CZAPEK, FRIEDRICH, Die Wirkung verschiedener Neigungslagen auf den Geotropismus parallelotroper Organe. Jahrb. Wiss. Bot. **43**:145–175. 1906.

[8] ZALESKI, W., Über die Rolle der Enzyme bei der Umwandlung organischer Phosporverbindungen in keimenden Samen. Ber. Deutsch. Bot. Gesells. **24**:285–291. 1906.

[9] ———, Zur Frage über den Einfluss der Temperatur auf die Eiweisszersetzung und Asparaginbildung der Samen während der Keimung. Ber. Deutsch. Bot. Gesells. **24**:292–5. 1906.

These two titles are excellent examples of over-minuteness—a fault to be avoided for the sake of those who have to cite the papers in future years.

[10] SCHREINER, OSWALD, and FAILYER, GEORGE H., The absorption of phosphates and potassium by soils. Bureau of Soils, U. S. Department of Agriculture, Bull. 32. 1906.

Scion and stock.—By grafting *Nicotiana Tabacum* on *N. affinis* (which contains little or no nicotin), and *N. affinis* on *N. Tabacum*, GRAFE and LINSBAUER have succeeded in showing,[11] in a more convincing way than before, the effect of the scion on the stock in respect to products of metabolism. Nicotin was found abundantly in *N. affinis*, whether it was functioning as stock or scion. Indeed, it attained almost the maximum amount found in *N. Tabacum* and scarcely fell below the limits of variation in that species. When *N. Tabacum* was the stock, and the scion, *N. affinis* was cut away completely, the new shoots produced contained even less nicotin than the *N. affinis* leaves had; so that the authors believe the scion had even increased the capacity of the *N. Tabacum* stock to form this alkaloid. Further researches are in progress.—C. R. B.

Tobacco.—In a long and somewhat controversial paper, excellently illustrated by halftones of various races of tobacco, ANASTASIA[12] concludes that there are four varieties within which may be grouped all the races of commerce. Three of these, vv. *havanensis, brasiliensis,* and *virginica,* are the offspring of *Nicotiana Tabacum,* and one owes its origin to hybridization between *N. Tabacum* and an unknown species of Nicotiana. Dr. ANASTASIA is desirous of securing seeds of certain races cultivated in the U. S. We bespeak the coöperation of those living in tobacco-raising sections. He may be addressed at the Experiment Station, Scafati, Salerno, Italy.—C. R. B.

Phototropism.—Further proof that the epidermal cells of phototropic leaves act as lenses, thus enabling them to function as receptive organs for adjustments to light, is adduced by HABERLANDT[13]. On covering young leaves of *Begonia semperflorens* with a layer of water, held in place by thin mica, he found no response to oblique light, though control leaves had attained the usual transverse posture, and the water-covered leaves gained it, though not perfectly, after removal of the layer of water.—C. R. B.

Solution cultures.—BREAZEALE[14] finds that transpiration and size of wheat seedlings are increased by the presence of sodium in nutrient solutions containing all other necessary elements. Further, the previous presence of sodium in a nutrient solution decreases the amount of potassium entering the plant during a subsequent period. The paper shows very little consideration for the reader. RAYMOND H. POND.

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[11] GRAFE, V., and LINSBAUER, K., Über die wechselseitige Beeinflussung von *Nicotiana Tabacum* und *N. affinis* bei der Pfropfung. Ber. Deutsch. Bot. Gesells. **24**:368–71. 1906.

[12] ANASTASIA, G. EMILIO, Le varietà typiche della *Nicotiana Tabacum* L. R. Istituto Sperimentale Tabacchi in Scafati. Ministero delle Finanze. Imp. 8vo. pp. 122. *figs.* and *plates 31.* 1906.

[13] HABERLANDT, G., Ein experimentaler Beweis für die Bedeutung der papillosen Laubblattepidermis als Lichtsinnesorgan. Ber. Deutsch, Bot. Gesells. **24**:361–6. 1906.

[14] BREAZEALE, J. F., The relation of sodium to potassium in soil and solution cultures. Journ. Amer. Chem. Soc. **37**:1013–1025. 1906.

NEWS.

DURING 1905 Kew Herbarium received in gifts over 16,000 sheets from about one hundred persons and institutions, and purchased nearly 7,000 sheets.

RAYMOND H. POND, Northwestern University, has been awarded a research scholarship at the New York Botanical Garden for six months, beginning on October 1.

THE BOTANICAL DEPARTMENT of the Universitv of Illinois has purchased the herbarium of GEORGE D. McDONALD, of Peoria, Ill. It contains about 12,000 specimens.—*Science.*

VERNON H. BLACKMAN, for ten years in the Department of Botany of the British Museum, has resigned this position to become Lecturer in Botany at the Birkbeck Institute. He also holds a lectureship at the East London College.

IN *Botanisches Centralblatt* (**102**: 367. 1906) there is published a short biographical sketch of the late Professor H. MARSHALL WARD, prepared by Professor S. H. VINES; and another notice appears in the *Kew Bulletin* (1906: 281), by L. A. BOODLE.

AN APPRECIATIVE NOTICE of the life and work of the late C. B. CLARKE appears in *Bulletin de l'Herbier* for September 1906, prepared by CASIMIR DECANDOLLE. Another biographical sketch of CLARKE, unsigned and including bibliography, is published in *Kew Bulletin* (**1906**: 271–281).

IN *Journal of Botany* for October 1906 there appears a biographical sketch of WILLIAM MITTEN, the bryologist, prepared by W. B. HEMSLEY, and accompanied by an excellent portrait. He died July 27, 1906, in his eighty-seventh year. The same number also contains a portrait of ROBERT BROWN. Another sketch of MITTEN by Helmsley is published in *Kew Bulletin* (**1906**: 283).

A GENERAL ACCOUNT of the work of Section K at the York meeting of the British Association is published in *Nature* of October 4. There were three appointed discussions upon the following topics: Some aspects of the present position of paleozoic botany, opened by D. H. SCOTT; The nature of fertilization, opened by V. H. BLACKMAN; The phylogenetic value of the vascular structure of seedlings, papers being read by a number of botanists whose names are identified with this phase of work.

WITH THE first part of volume 96, issued late in March, the publication of *Flora* passed into the hands of the well-known house of GUSTAV FISCHER. Hereafter the volumes will be enlarged to at least 560 pages, without increase in price, and the designation of *Erganzungsbände* will be abandoned. Fortunately they were always numbered consecutively with the others, and so the superfluous name made little bibliographic confusion. No reviews of literature are to appear in future. Articles are to be restricted in length as a rule to 48 pages, and for this the editor clears his desk by getting in the tenth of his *Archegoniatenstudien* as the leader of the new volume, a paper of over 200 pages!

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Editors: JOHN M. COULTER and CHARLES R. BARNES

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CURRENT LITERATURE

Communications for the Editors should be addressed to them at the University of Chicago, Chicago, Ill.

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DECEMBER 1906

THE LIFE HISTORY OF POLYSIPHONIA VIOLACEA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXXXVII.

SHIGEO YAMANOUCHI.

(WITH THREE DIAGRAMS AND PLATES XIX–XXVIII)

INTRODUCTION.

THERE have been published by various authors many accounts of investigations on the red algae treating of the morphology of the thallus, the development of the cystocarp, and tetraspore formation. The first general studies on the reproductive processes in the group were those of BORNET and THURET (**12**) and JANCZEWSKI (**43**). These papers have never been surpassed in clearness of expression and beauty of illustration, but they considered simply the outer morphology or histology and gave no cytological details of fertilization, nor did they trace the life history. SCHMITZ (**69**) published an account of the fructifications of more than forty species in various groups of the red algae, giving special attention to the auxiliary cells, but in his conclusions he failed to distinguish between the act of fertilization and the secondary fusions concerned with the auxiliary cells, and he developed elaborate speculations in which these fusions were included as a part of the sexual process. This misconception was cleared up by OLTMANNS' discovery (**55**) that the real sexual act is the union of male and female gamete nuclei in the carpogonium, and that the auxiliary cells are probably only concerned with the nourishment of the cystocarp. OLTMANNS was the first author to develop the theory that the structure derived from the fertilized carpogonium was sporophytic in character; however, he presented no cytological evidence for this view. WOLFE (**86**) placed this theory of OLTMANNS on a cytological basis by showing that the cystocarp of Nemalion contained nuclei with double the number of chromosomes found in the sexual plants or gametophytes. However, WOLFE did not give a detailed account of the period of chromosome reduction. Nemalion is one of the simplest types of the red algae. There are no auxiliary cells or tetraspores, at least on the American plants so far as known; consequently the life history is very much simpler than that of the higher forms. The behavior of the auxiliary cell nucleus during the development of the cystocarp has been studied by OLTMANNS (**55**) with especial clearness in Callithamnion and Dudresnaya, but the structural difference between the nuclei of auxiliary cells (gametophytic) and those derived from the fertilized carpogonium (sporophytic) was not determined by him. Moreover, as regards the real nature of the tetraspore, so characteristic of the red algae, there has been no cytological work except a study of nuclear division in Corallina by DAVIS (**18**).

The significance of the tetraspore in the life history was not known. Various authors have presented speculations upon the subject; for example, OLTMANNS (**55**) regarded the tetraspore as an asexual reproductive structure comparable to brood organs or gemmae, having no fixed place in the life cycle, and STRASBURGER has followed this interpretation.

This investigation was begun in the hope that some of these problems might be solved by carefully following the life history of a type with particular attention to the behavior of the nucleus at critical periods. Although red algae include a wide range of types, the nature of the tetraspore and the history of the life cycle where tetraspores are present have probably been determined by this investigation of the ontogeny of *Polysiphonia violacea* Grev., except in forms where abnormalities may be present, due perhaps to apogamy or apospory.

As stated in a preliminary paper (YAMANOUCHI **87**), the material was collected at Woods Hole, Mass., during July and August 1905, where cultures of the carpospores and tetraspores were made to obtain stages in their germination. The method of killing, fixing, imbedding, cutting, and staining are given in that preliminary note.

This paper presents first the results of my studies of the mitosis in germinating tetraspores and carpospores and in the vegetative cells of mature plants; then comes an account of spermatogenesis, formation of procarp, fertilization, and development of the cystocarp; tetraspore formation is then considered, followed by a description of certain abnormalities; finally, there is a discussion of the cytological phenomena and alternation of generations. This last topic has been given considerable attention, for the chief results of this investigation have been the establishment of an antithetic alternation of generations in Polysiphonia, with the period of chromosome reduction at the time of tetraspore formation.

The investigation was begun during the summer of 1905 at the suggestion of Dr. BRADLEY M. DAVIS during my stay as an occupant of a Carnegie research table at the Marine Biological Laboratory, Woods Hole; and to the Carnegie Institution I wish to express my obligations for the privilege of the table. The studies were continued and completed by me in the Hull Botanical Laboratory as a Fellow of The University of Chicago, under the direction of Professor JOHN M. COULTER and Dr. CHARLES J. CHAMBERLAIN, the kind assistance and painstaking criticism of Dr. DAVIS continuing also throughout the whole progress of the investigation. To these gentlemen I am under great obligation; and also to the other members of the botanical staff of Hull Botanical Laboratory for courtesies extended to me in many ways.

THE FIRST MITOSIS IN THE GERMINATING TETRASPORE.

The tetraspore when discharged from the parent plant assumes a spherical form. Plastids usually lie near the periphery of the cell, whose cytoplasm presents an irregular, coarse alveolar structure, with the nucleus lying near the center. The cytoplasm surrounding the nuclear membrane is a finer network than anywhere else in the cell. Within the nucleus there is a very delicate linin mesh dotted here and there with chromatic granules (*fig. 1*). From the fact that the transverse walls of the cytoplasmic alveoli end on the nuclear membrane at points where the linin threads start, it seems possible that there exists a close physiological relation between these structures. The nucleus generally contains a single nucleolus, variously situated and homogeneous in structure, but sometimes two nucleoli are present.

Preliminary to mitosis, the delicate network becomes somewhat coarser and the thread somewhat broader, and gradually in many different parts the chromatin granules appear in irregular rows as chains of beads of different lengths. There are about 20 of these chains, as illustrated in *figs. 2a–2c*, which represent three sections of the same nucleus. They are the beginnings of the chromosomes, similar to the prochromosomes described by OVERTON (**58**) in the presynaptic stage in the pollen mother cells of Thalictrum and three other species of flowering plants. The material which accumulates in these prochromosomes must come from the chromatin granules imbedded in the linin thread, for it is evident that the nucleolus does not contribute any material directly to their formation. This behavior is therefore similar to the process of chromosome formation in higher plants, and is very different from the condition reported by WOLFE (**86**) for Nemalion, where the chromosomes are described as coming out from the nucleolus. The nucleolus of Polysiphonia remains unchanged while the prochromosomes are being formed. These prochromosomes gradually become more pronounced, increase in breadth, and the bead-like structure is transformed into the more homogeneous rod-shaped chromosomes that become distributed through the whole nuclear cavity attached to a linin thread, as shown in *figs. 3a* and *3b*, which represent two sections of the same nucleus. The nucleolus may remain undivided or fragment into two at this time.

The cytoplasm around the resting nuclear membrane appears at first homogeneous, but during prophase there is a gradual accumulation on the two opposite sides of the nucleus, and finally two deeply staining centrosome-like bodies appear, forming the poles of the more slightly elongated nucleus (*fig. 4*). While these changes in the cytoplasm are going on without the nucleus, some important events take place within. The chromosomes become thickened and more compact and gather in the middle region of the nuclear cavity, with linin threads still attached to their ends, and at last they are arranged in the equatorial plate (*fig. 5*). The nuclear membrane is still present when the spindle is developed (*fig. 5*), so that the latter is consequently intranuclear.

It is very interesting to compare this stage with the previous one (*fig. 4*), taking into consideration the kinoplasmic centers, the shape of the nuclear cavity, and the spindle. As regards the centers of kinoplasmic activity, in the preceding stage the kinoplasm is shown in the process of accumulation at the two poles, and a single clearly differentiated granule may be interpreted as the first visible indication of approaching spindle formation. At the time when the equatorial plate is formed, the kinoplasmic material becomes massed more densely than before, and two very large centrosphere-like structures are differentiated at the poles of the spindle (*figs. 5, 6*). These kinoplasmic bodies have a compact, well-defined form, but are without radiation. The nuclear cavity at the stage of metaphase is smaller than before, and the poles of the spindle become drawn closer together. The development of the spindle proved very difficult to study, and its history is discussed later in the paper under the head of spindle formation.

The accumulations of kinoplasm at the poles of the spindle are very characteristic and resemble the centrospheres described by DAVIS (**18**) in the tetraspore mother cell of Corallina, except that the latter have well-defined radiations. The chromosomes when arranged in the equatorial plate are readily counted if viewed in transverse sections of the spindle (*fig. 7*), as well as during prophase (*figs. 3a, 3b*), and the number is clearly 20. Granular fragments of the nucleolus are always present in the nuclear cavity during the metaphase, after which they disappear.

The duration of metaphase is rather long and the centrosphere-like structures persist until late anaphase. When each group of daughter chromosomes passes to the pole of the spindle, there are left only a few fibrils forming a central spindle between them (*fig. 8*). After anaphase the kinoplasm intrudes into the nuclear cavity and the central spindle gradually disappears (*fig. 9*). The kinoplasm thus surrounds the groups of daughter chromosomes, and the centrosphere-like structure loses its distinct differentiation and becomes a cloudy mass of kinoplasm without a clearly defined boundary (*fig. 9*).

Each group of daughter chromosomes, which during anaphase had a flattened form, becomes more or less spherical, with a small space within (*fig. 10*). The mass of chromosomes surrounded by granular kinoplasm comes to lie in nuclear sap or caryolymph, and it seems possible that the nuclear membrane may be formed as the result of the contact of the caryolymph with the surrounding cytoplasm (*fig. 11*). Such conclusions were drawn by LAWSON (**44**) and GRÉGOIRE and WYGAERTS (**36**) in their studies of the telophase of mitosis. The chromosomes later lose their individual outlines and the mass becomes transformed into a chromatin network (*fig. 12*). A new nucleolus is then formed in the daughter nucleus.

No mention has yet been made of the manner of cell division. The coarse alveolar structure of the cytoplasm taken as a whole persists during mitosis, the kinoplasm associated with the division of the nucleus remaining distinct from the alveolar cytoplasm and reacting more deeply to the plasma stains. The daughter nuclei when formed lie above one another in the germinating tetraspore. Before they have attained their full size a cleavage furrow appears at the middle region of the cell which is at first very shallow. The central spindle that lay between the two groups of daughter chromosomes has entirely disappeared before the cleavage furrow is formed, so that the center of the cell is filled by cytoplasm which presents a very coarse alveolar structure, especially in the middle region, where the cleavage furrow begins (*fig. 13*). This furrow proceeds inward, the only visible assistance in its development being the extensive fusion of vacuoles by the breaking of their limiting membranes so that less resistance is presented to its progress. Finally, the furrow reaches nearly to the center of the cell (*fig. 14*), so that the tetraspore becomes divided into daughter cells, which are in communication by a strand of protoplasm, as is so generally characteristic of the red algae.

THE FIRST MITOSIS IN THE GERMINATING CARPOSPORE.

The carpospore on its escape from the cystocarp is somewhat pear-shaped, but it gradually assumes an oblong or spherical form while floating in the water. The coarse alveolar structure of the cytoplasm, the arrangement of the plastids, and the fine linin network within the nucleus (*fig. 15*) are similar to those of the tetraspore. Moreover, the first mitosis takes place at about the same period after their escape from parent plants, namely after about fifteen hours.

The history of the mitosis in the germinating carpospore is so similar to that in the tetraspore that it seems best to point out only the marked differences between the two. The delicate linin network within the nucleus passes into a coarse chromatin reticulum upon which chains of chromatin granules appear here and there (*figs. 16a–16c*), and these are prochromosomes, as illustrated in the preceding figures of the tetraspore (*figs. 2a–2c*). The number of prochromosomes, however, is 40, and consequently double the number in the germinating tetraspore. The 40 prochromosomes grow more and more homogeneous in structure and finally become elongated chromosomes (*figs. 17a, 17b*). The weakly staining linin network disappears, but short threads remain attached at the ends of chromosomes. The kinoplasm surrounding the nuclear membrane becomes accumulated at the two poles of the nucleus, where a centrosome-like body may always be found (*fig. 18a*), and this accumulation of kinoplasm proceeds still further until there are two conspicuous centrosphere-like structures differentiated at metaphase (*fig. 19*). The spindle is somewhat larger and broader than that in the tetraspore, because of the double number of chromosomes (*fig. 19*). The polar view of that stage (*fig. 20*) clearly shows the number 40.

The nucleolus fragments during metaphase, the portions lying beside the spindle (*fig. 19*) and sometimes remaining until anaphase, after which they disappear. The behavior of the daughter chromosomes after anaphase is the same as during mitosis in the tetraspore; the groups of daughter chromosomes gather at the poles of the spindle (*fig. 21*) and become surrounded by granular kinoplasm (*fig. 22*). At the time of the formation of the nuclear membrane, the chromosomes may still be recognized and estimated as 40 (*figs. 23a, 23b*). The daughter nuclei increase in size by the secretion of nuclear sap (*figs. 24a–24c*), and finally the chromatin becomes distributed over a linin network in the resting nucleus (*fig. 25*). The germinating carpospore becomes divided by a cleavage furrow in a similar manner to that of the tetraspore.

The second and third mitosis in both germinating tetraspore and carpospore were also studied, and they were similar to those of the first divisions, showing always the two essential differences in the number of chromosomes.

MITOSIS IN THE VEGETATIVE CELLS OF THE MALE, FEMALE, AND TETRASPORIC PLANTS.

To make sure of the number of chromosomes contained within the nuclei throughout the life history, the mitoses in vegetative cells of the three forms of Polysiphonia plants—male, female, and tetrasporic—were studied. The following is a very brief account of the essential features of these mitoses.

The nuclei in the apical cells of any of the three forms of plants are somewhat larger in size than those in older region of the thallus; but although it is not difficult to obtain the successive stages of mitosis in older parts, the nucleus of the apical cell is somewhat more favorable for study and will be used in this description.

The cytoplasm in the apical cell shows very fine alveolar structure, the plastids lie near the wall, and the nucleus in the resting stage resembles that in the germinating carpospore and tetraspore (*figs. 26, 45*). The linin network becomes coarser (*figs. 27, 46*), and finally in the case of the male (*figs. 28, 29*) and female plants (*fig. 36*) 20 chromosomes appear, whereas in the tetrasporic plant (*fig. 47*) 40 chromosomes are present. The chromosomes may be readily counted at metaphase in polar views of equatorial plates, when it is evident that the sexual plants have 20 (*figs. 31, 38*) and the tetrasporic plants 40 (*fig. 50*). In spite of the small size of the nuclei, kinoplasmic accumulations at opposite poles of the nucleus are evident during prophase, and deeply staining centrosome-like bodies are conspicuous at the poles just before the spindle is formed (*figs. 29, 36*). Centrosphere-like structures are very conspicuous at the poles of the spindle during metaphase (*figs. 30, 37, 48*). These structures are more clearly shown in the mitosis in older regions of the thallus. *Fig. 43* illustrates such a mitosis from a female plant, those of the male and tetrasporic plants being omitted to avoid repetition. The smaller size of the nuclear cavity during metaphase is as constant a character of these mitoses as of those in the tetraspores and carpospores. After metaphase the two sets of daughter chromosomes remain included in the old nuclear membrane for a while (*figs. 32, 39, 49*). During the anaphase the groups become further separated, the nuclear membrane disappears, and a large vacuole intrudes between them (*figs. 33, 41, 51*). When the daughter nuclei are completely formed, a cleavage furrow develops at the periphery in the middle region of the cell (*figs. 35, 42*), a large vacuole being present in the center. The mechanism of constriction by the cleavage furrow is probably greatly assisted by the presence of this single vacuole, in place of numbers of smaller ones which are found in the tetraspores and carpospores.

SPERMATOGENESIS.

The sperms or spermatia are formed normally on special short branches called antheridia, which are developed in clusters at the tips of the main filaments. The antheridium consists of an axial siphon (*diagram 1*) which becomes surrounded and covered by a large number of small cells. These generally develop sperm mother cells at the periphery of the antheridium, and may consequently be called "stalk cells." The mitoses in the axial siphon of the antheridium were studied (*fig. 52*), as well as those which form the stalk cells (*fig. 53*), and they showed the number of chromosomes to be 20. The methods of chromosome formation, the development of the intranuclear spindle, and the cell division by constriction are the same as those of the vegetative cells already described.

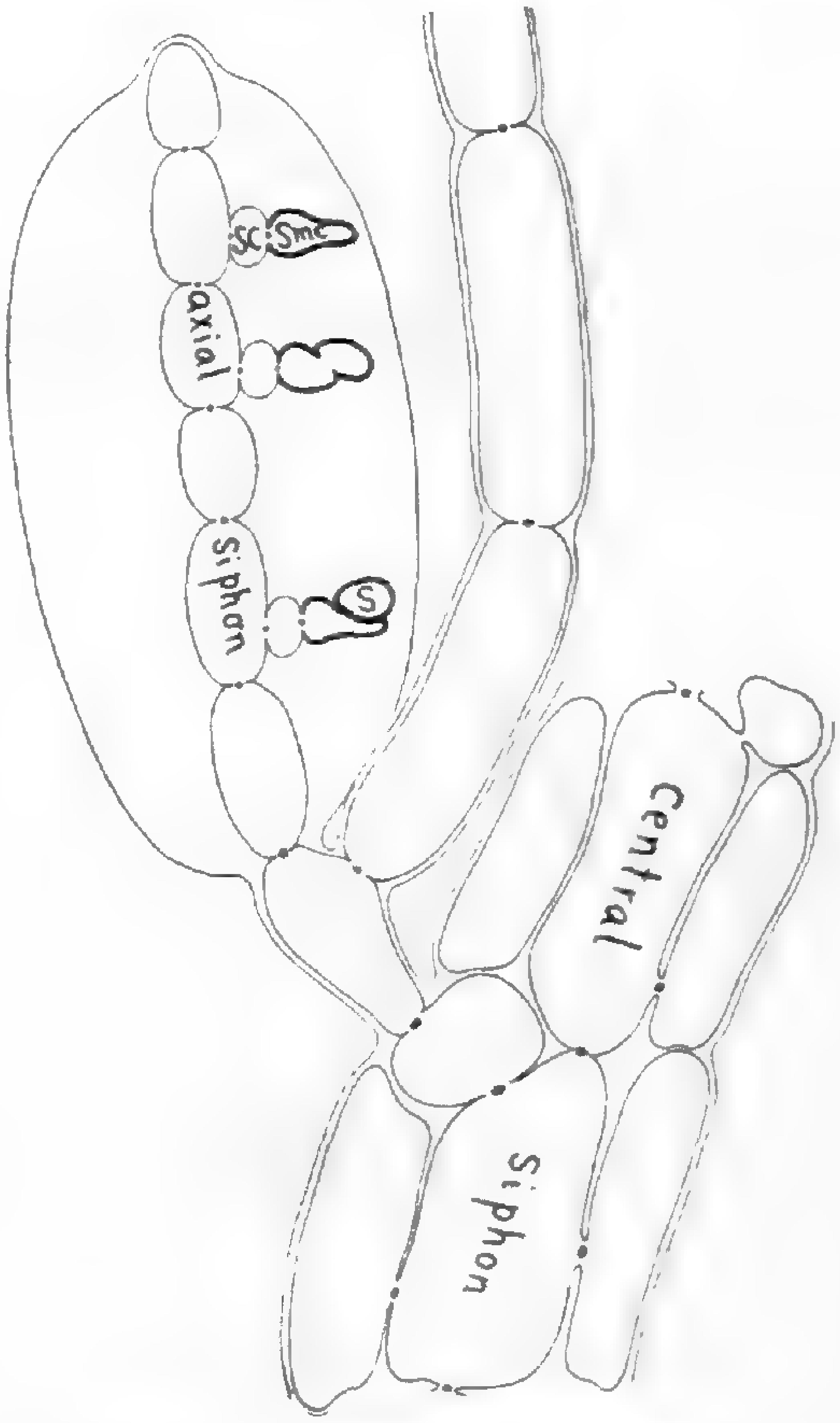

DIAGRAM 1.—Section of an antheridium, showing position of axial siphon, stalk cell (*sc*), sperm mother cell (*smc*), and development of the sperm (*s*).

The formation of the sperm mother cells from the stalk cells (*fig. 54*) is illustrated in *figs. 55–61*. *Fig. 55* presents the prophase of of the mitosis, *fig. 56* metaphase, *fig. 57* the equatorial plate viewed from a pole, *fig. 58* shows anaphase, and *figs. 59* and *60* illustrate telophase. The cell division by constriction is shown in *fig. 61*. The sperm mother cell (*fig. 62*) increases in size and assumes its characteristic form, which is narrow at the periphery and swollen at the base. In rare cases the formation of the stalk cell is omitted,
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so that sperm mother cells are developed directly from the axial siphon of the antheridium.

The cytoplasm of the sperm mother cell (*fig. 62*) has a very delicate granular structure and is generally destitute of plastids. The nucleus in the resting state contains a fine network and a nucleolus. Prochromosomes, 20 in number, are formed in the network (*figs. 63, 63a*) and are connected by weakly staining linin threads. The prochromosomes increase in size and become rod-shaped chromosomes (*figs. 64, 64a*).

Kinoplasm becomes differentiated from the surrounding cytoplasm and accumulates at the poles of the elongating nucleus, and a centrosome-like body appears at each pole (*figs. 64, 64a*). The stage of prophase passes into metaphase (*figs. 65, 65a*), when centrosphere-like structures are well-developed and the axis of the spindle is shorter than the diameter of the equatorial plate, as is the case during the mitoses within the carpospores, tetraspores, and vegetative cells. The number of chromosomes is clearly 20 in this mitosis, as shown in polar view of the equatorial plate (*fig. 66*). The nuclear membrane is present during metaphase (*fig. 67*), and as the two groups of daughter chromosomes separate a vacuole intrudes between them (*figs. 68, 69, 70*). The centrosphere-like structures are not recognizable after metaphase. The set of daughter chromosomes which passes to the basal region of the cell becomes aggregated, surrounded by a nuclear membrane, and enters into a resting condition; while the chromosomes of the other set, passing to the upper part of the cell still retain their individuality, although it is probable that a very delicate membrane may be formed (*fig. 70*).

A cleavage furrow in the middle region of the cells appears (*fig. 71*), and by the same mechanism as in the case of vegetative cells effects a separation of the upper half as a sperm cell from the lower half. The greater part of the large vacuole is included in the sperm, which consequently has a relatively small amount of protoplasm in comparison with its size (*figs. 72, 73*). The cleavage furrow which cuts off the sperm cell crosses the sperm mother cell obliquely, and consequently the sperm assumes a lateral position, allowing the sperm mother cell to elongate. When the matured sperm is detached completely from the sperm mother cell, the latter has assumed again its characteristic extended form (*fig. 75*).

The sperm when detached is oval in form (*fig. 73*), and has a thin wall derived from the mother cell, and a large vacuole occupies almost all the cell cavity. The cytoplasm is therefore forced to lie in a thin layer under the cell wall, and the nucleus occupies the larger end of the oval. The chromosomes maintain their individuality and are connected with one another by delicate linin threads (*figs. 74, 74a*).

The nucleus remaining in the sperm mother cell after the formation of the first sperm divides at once, passing through prophase (*fig. 75*), metaphase (*figs. 76, 78*), and anaphase stages (*figs. 79, 80*), following the same history as in the previous mitoses. Here is apparent also the same conspicuous difference in the form of the nucleus between prophase and metaphase (*figs. 75, 76*), 20 chromosomes (*fig. 77*) always appearing in this critical stage. Finally, the telophase of mitosis is followed by cell division through a cleavage furrow, which cuts off the second sperm (*fig. 81*) in a similar manner to the first. The nucleus which remains in the sperm mother cell may repeat the process, forming a third sperm.

The successive formation of sperms by constriction from the sperm mother cell may be compared, in a general way at least, to the process of formation of conidia in certain groups of fungi, where the conidia are developed successively by constriction from a conidiophore. Of course such a comparison is a superficial one, since conidia are by no means comparable to sperms in the phylogenetic sense. The spermatia found in the rusts and lichens, and certain antheridia of the Laboulbeniaceae present greater resemblances. THAXTER (**78**) describes an exogenous method of sperm formation in Ceratomyces and Zodiomyces, in which sperms are developed successively from a definite point at the distal end of fertile cells of the antheridial branches, agreeing thus with the process in Polysiphonia.

WOLFE (**86**) considers the sperm of Nemalion to be the homologue of an antheridium because the sperm nucleus divides into two. No mitosis was found in the sperm of Polysiphonia, although this matter received careful attention. The sperm of Nemalion also escapes as a naked or thin-walled protoplast from the parent cell-membrane, while that of Polysiphonia becomes detached and retains the parent cell wall. The differences, however, do not seem to the author to affect the relationship of these two sperms as homologous structures. That of Polysiphonia is also the homologue of a unicellular antheridium, in which mitosis, if ever present, has been suppressed, and the cell as a unit has become the male sexual element.

FORMATION OF THE PROCARP.

Development of the carpogonial branch.—The female organ or procarp consists in the beginning of a short branch of three or four cells. The most important of these is a cell of the axial siphon which lies next to the apical cell (*diagram 2, A*). This cell increases in size more rapidly than do the adjacent cells of the filament, so that it is very easy to recognize the primordium of the female organ, and divides successively to form five peripheral cells, which finally completely surround it (*diagram 2, B*). The first stage is illustrated in *figs. 82–84* and the second in *figs. 85–87*. The third and fourth divisions of the siphon cell have not been figured, but they occur in such a manner that the third and fourth peripheral cells are formed opposite each other and between the first and second (*diagram 2, B*). The fifth division gives rise to a peripheral cell between the first and the fourth, which later develops the carpogonial branch and has been called the pericentral cell.

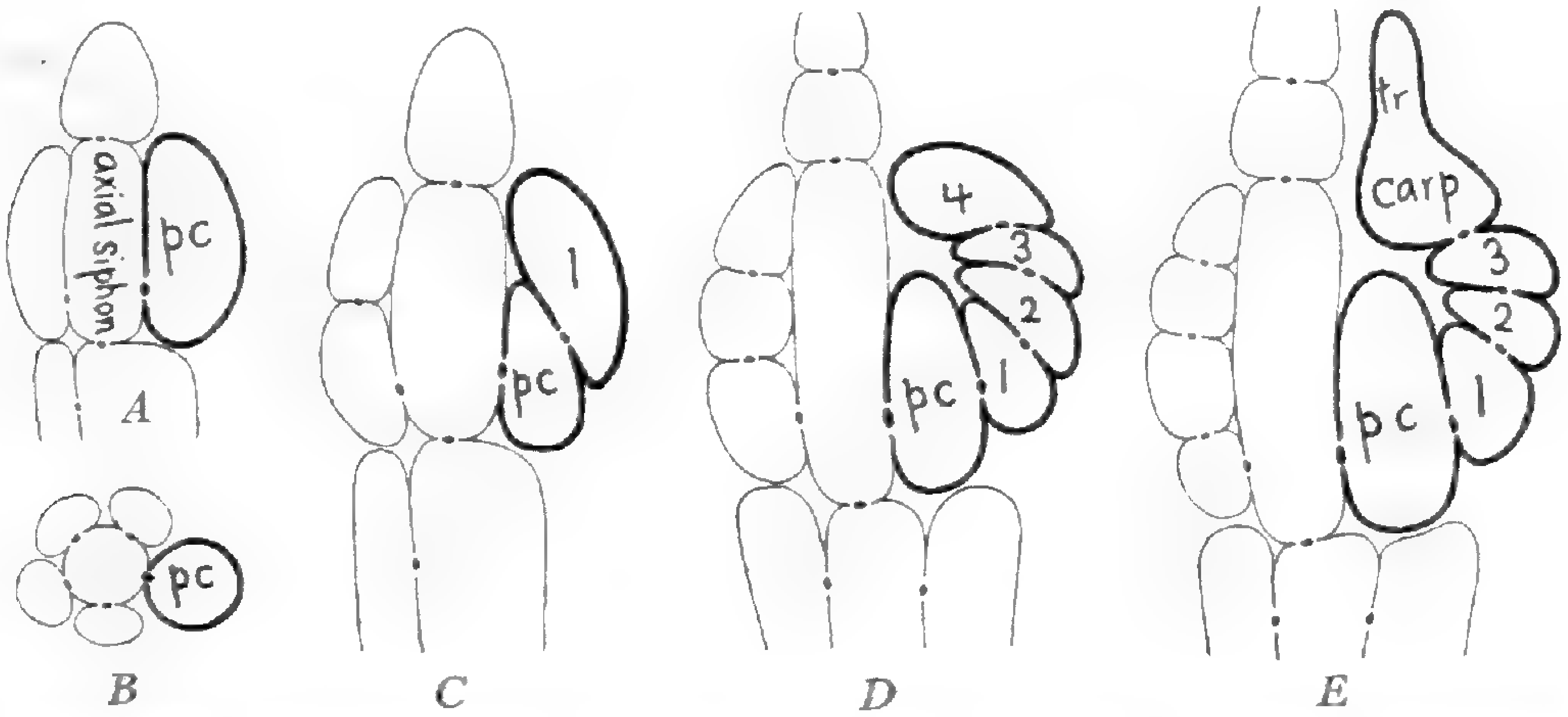


DIAGRAM 2.—Development of the carpogonial branch: *A*, young procarp with pericentral cell (*pc*); *B*, cross section of *A*; *C*, formation of first cell of carpogonial branch; *D*, the four cells of carpogonial branch; *E*, development of trichogyne (*tr*) from fourth cell or carpogonium (*carp*) of the carpogonial branch.

During every nuclear division concerned with the formation of the peripheral cells, 20 chromosomes constantly appear, as shown in polar views (*figs. 83, 86*), and this number is passed over to the pericentral cell. The nucleus in the pericentral cell divides in a direction nearly parallel to the axis of the procarp (*figs. 89–93*), cutting off a cell which develops the carpogonial branch (*diagram 2, C*). The pericentral cell later also gives rise to a group of auxiliary cells. The carpogonial branch consists of four cells which are formed successively as shown in *diagram 2, D, E.* It is somewhat bent, so that the terminal cell lies almost above the pericentral cell. This terminal cell becomes the carpogonium and develops the trichogyne. The mitoses concerned with the development of the carpogonial branch are illustrated in *figs. 94–99,* and invariably showed 20 chromosomes at metaphase. As the result of these successive mitoses, the carpogonial branch extends at one side of the central axial cell, with the pericentral cell situated between them (*diagram 2, E*).

The nucleus in the fourth or terminal cell of the carpogonial branch divides (*fig. 100*) to form two nuclei (*fig. 101*), each with 20 chromosomes, one of which becomes the female gamete nucleus, while the other enters the trichogyne that is formed at once. The upper end of the cell pushes out as a delicate process which contains almost from the beginning one of the two nuclei, the other remaining in the basal swollen region of the cell called the carpogonium (*figs. 102, 103, 104*), which corresponds to an oogonium. The formation of the trichogyne completes the development of the female organ, whose parts in longitudinal section are shown in *fig. 103.*

The trichogyne.—The trichogyne nucleus, as a rule, is situated in the middle region of the trichogyne, which has about the same breadth throughout its tubular cavity, but becomes constricted below where it joins the carpogonium. No plastids could be found in the trichogyne.

The presence of a trichogyne nucleus in the red algae has been a subject of some controversy. SCHMITZ (**69**) described a large single or several small granular bodies, which stained like chromatin, in the trichogyne of *Batrachospermum moniliforme* and Gloeosiphonia before fertilization, but he gives no interpretation further than the few words, "Derivate des Zellkerns der weiblichen Zellen?" Eight years later DAVIS (**17**) observed in the same species of Batrachospermum an unmistakable nucleus in the trichogyne, staining with haematoxylin as a dark blue body. OLTMANNS (**55**) also observed the granule within the trichogyne of Gloeosiphonia, but he regarded it as having no connection with the nucleus. SCHMIDLE (**68**) failed to find the nucleus in the trichogyne of Batrachospermum, and OSTERHOUT (**57**) contends that it is not present. WOLFE (**86**) observed a nucleus in the trichogyne of Nemalion, which he assumes to be derived from the young carpogonium, although the mitotic figure was not found. The presence of a nucleus in the trichogyne necessitates a modification of our conception of the morphology of the female organ in the red algae.

The earlier conception of the morphology of the trichogyne as given by SCHMITZ (**69**) was a cytoplasmic extension of the carpogonium, developed as the receptive organ for the sperm. This conception was followed by OLTMANNS (**55**), SCHMIDLE (**68**), and OSTERHOUT (**57**). DAVIS (**17**), however, concluded that the trichogyne is not a cytoplasmic extension from the carpogonium, but that it possesses a well-defined nucleus and hence has a certain degree of independence. The trichogyne of Batrachospermum has certainly a body that must be regarded as a chromatophore. WOLFE'S studies of Nemalion (**86**) support this view with respect to a trichogyne nucleus. In Polysiphonia, as stated above, there is present a trichogyne nucleus whose origin has been traced to a division in the terminal cell of the carpogonial branch. These facts have an important bearing on the structure of the trichogyne in lichens and Laboulbeniaceae. THAXTER (**78**) has described multicellular branching trichogynes in certain forms of Laboulbeniaceae, and the long multicellular trichogyne of Collema (BAUER **6**) and Physcia (DARBISHIRE **16***a*) illustrate similar conditions. In the lower forms of algae where heterogamy is established, male and female gametes are generally formed in unicellular antheridia and oogonia. The female gametes having become non-motile, usually remain within the oogonium and are fertilized by motile male gametes which enter the oogonium through a pore, as is illustrated by Oedogonium. With the loss of motility on the part of the male gametes, a receptive region or structure seems to have been developed by the oogonium, and in this manner the trichogyne probably arose. However, the development of the trichogyne means that the female cell, which is the homologue of an oogonium, acts as a unit. Should there be in such a cell one or more mitoses, which are the remnants of ancient nuclear division when two or more gametes may have been developed, then the supernumerary nuclei would be expected to degenerate. This seems to be the condition in the red algae, where there is an extra nucleus beside the one which is in the gamete. This extra nucleus has an important relation to the development of the trichogyne, which consequently is much more than a mere cytoplasmic extension from the carpogonium; for having a nucleus it may possess the possibilities of a somewhat extensive development. This is perhaps the explanation of the multicellular trichogynes of the lichens and the Laboulbeniaceae, which in some forms of the latter group are extensively branched.

The passage of the sperm nucleus through the trichogyne into the carpogonium.—The nucleus of the carpogonium increases in size as the female cell matures, while the nucleus of the trichogyne remains about the same size as when it was formed (*fig. 104*). The sperm becomes attached to the tip of trichogyne (*fig. 105*). The walls between the two structures dissolve, and the contents of the sperm flows into the trichogyne (*fig. 106*). The sperm nucleus consists of a number of deeply staining bodies (about 20), which are chromosomes. The nuclear membrane if present must be very delicate, for it could not be positively recognized (*figs. 106–108*). The deeply staining sperm nucleus in the trichogyne is in sharp contrast with the smaller trichogyne nucleus whose chromatin content stains weakly. The sperm nucleus moves downward, passing the trichogyne nucleus (*figs. 107, 108*), and enters the carpogonium. The female nucleus in the carpogonium, which until this time lay at the bottom of the cell, seems to move upward a short distance as if to meet the sperm nucleus (*fig. 109a*). The two gamete nuclei are strikingly dissimilar at the time of union, the male consisting of a densely packed aggregation of chromosomes, while the female is larger and in a typical resting condition, with chromatin distributed over a linin network (*fig. 109a*).

The trichogyne nucleus may still be recognized after the sperm nucleus has passed into the carpogonium. However, the cytoplasm of the trichogyne soon shows signs of disorganization, first at the tip, and a little later the trichogyne nucleus breaks down. When the male nucleus is in contact with the female and becomes somewhat pressed against it, the cytoplasm of the trichogyne has probably always separated from the carpogonium and the trichogyne has begun to shrivel.

Formation of the auxiliary cells.—Parallel with the fusion of the gamete nuclei there takes place the development of a set of auxiliary cells, as shown in *diagram 3*. The pericentral cell, which was the progenitor of the carpogonial branch and lies beneath the carpogonium (because of the growth and bending of this structure), now gives rise to two cells (*diagram 3, a1, a'1*), one somewhat below and the other at the side. The cell below divides once (*diagram 3, a'1, a'2*). The cell at the side develops a branching group which lies close beside the carpogonial branch, as shown in *diagram 3* (*a 1, a 2, a 2', a 3, a 3'*). One of these auxiliary cells (*a 3*) is formed between the fertilized carpogonium and the pericentral cell. Thus the final result is two series of auxiliary cells, one consisting of five, the other of two cells; and in the former series it should be remembered that one of them has an important function, as will appear later, becoming the path of communication between the fertilized carpogonium and the pericentral cell.

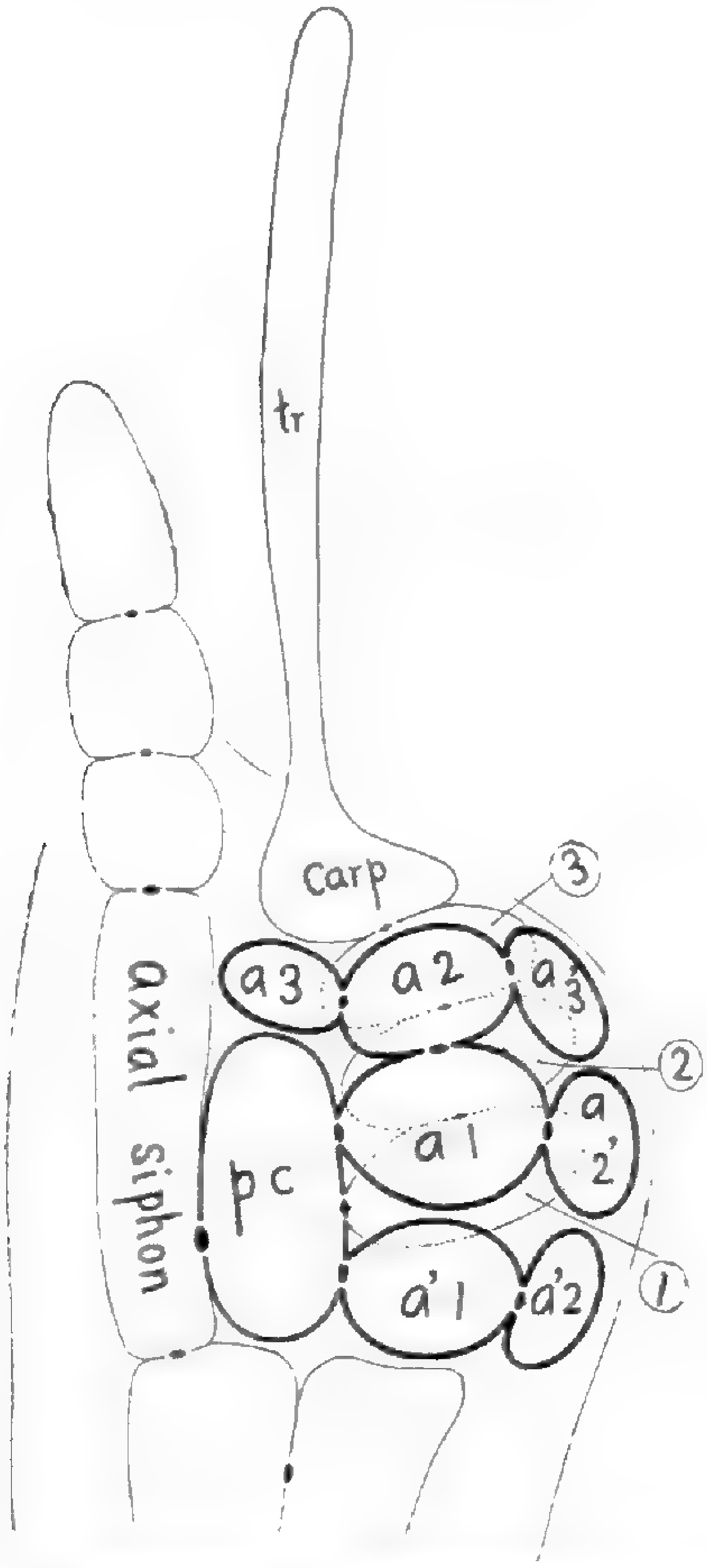


DIAGRAM 3.—Mature procarp showing arrangement of auxiliary cells: *pc*, pericentral cell; *a1*, *a2*, *a2'*, *a3*, *a3'*, *a'1*, *a'2*, auxiliary cells; 1, 2, 3, cells of carpogonial branch; *carp*, carpogonium; *tr*, trichogyne.

PHILLIPS (**60**) in his studies on the Rhodomelaceae recognized many features in the structure of the procarp of Polysiphonia which I have just described. His account of a four-celled carpogonial branch is correct, together with the general account of the formation of the central cell, as will be described presently. However, I was not able to find the arrangement of the auxiliary cells as he has described them, and his investigation lacks the cytological details through which the nuclei that enter the carpospore must be traced.

FERTILIZATION AND DEVELOPMENT OF THE CYSTOCARP.

The fusion of the gamete nuclei.—The male and female gamete nuclei which met in the carpogonium have generally fused by the time the auxiliary cells are formed. The membrane of the female nucleus appears to dissolve at its point of contact with the sperm nucleus, which lies closely pressed against it (*fig. 114a*), and later the chromatin content of the male nucleus enters the female (*fig. 115a*). The subsequent changes in the female nucleus result in the gradual transformation of its linin network into clearly defined chromatin granules and finally into chromosomes. At the same time the crowded group of male chromosomes (*fig. 115a*) becomes looser, the chromosomes separating from one another, some remaining near the periphery of the fusion nucleus, and some passing into the interior. Finally the chromosomes derived from male and female nuclei become mingled together and the fusion nucleus assumes the appearance of prophase (*fig. 116*).

The first mitosis of the fusion nucleus (*sporophytic*).—The fusion nucleus which results from the union of the male and female gamete nuclei now passes into the prophase of mitosis. The number of chromosomes is 40, which is of course double the number in the sexual plants or gametophytes, so that the fusion nucleus is sporophytic in character. These chromosomes differ from one another in size, and some of the smaller certainly come from the male nucleus. It would be interesting to trace carefully the history and behavior of these chromosomes, but I am not prepared at present to discuss this matter in detail.

The stages of prophase in Polysiphonia, as previously described, are always characterized by the presence of centrosphere-like structures at the poles; however, these structures do not seem to be present during the first mitosis of the fusion nucleus. The spindle of this mitosis is remarkable for its size and the breadth of the poles (*fig. 117a*). Another peculiarity is the fact that the nuclear membrane disappears during prophase, so that the spindle lies freely in the cytoplasm. It is possible that the early dissolution of the membrane is connected with the fusion of the gamete nuclei, which may weaken the membrane of the female nucleus. As regards the count of chromosomes, their number 40 is apparent when the equatorial plate is viewed from the pole (*fig. 118a*). In the late metaphase the same number may be estimated in both groups of daughter chromosomes (*fig. 123*), which means that this first division of the fusion nucleus is a typical mitosis. At anaphase there is present a rather conspicuous central spindle between the two sets of daughter chromosomes (*fig. 124a*).

The migration of sporophytic nuclei into the pericentral cell.—There is only one mitosis within the fertilized carpogonium. The carpogonium now fuses with the auxiliary cell, which lies between it and the pericentral cell (*diagram 3, a3*). The wall between these cells dissolves and a broad communication is formed connecting them. A fusion between this auxiliary cell and the pericentral cell follows at once, so that the carpogonium is then in free communication with the pericentral cell by means of the auxiliary cell. Sometimes this communication becomes established as early as the metaphase of the mitosis of the fusion nucleus. By means of the passage which is established by these cell unions, the two sporophytic daughter nuclei, resulting from the division of the fusion nucleus, move down into the pericentral cell (*figs. 125, 126*).

During the formation of the auxiliary cells from the pericentral cell each nucleus in the first three cells of the carpogonial branch divides (*figs. 119–122*). The daughter nuclei then lie side by side in pairs within the cells of the carpogonial branch. While the sporophytic fusion nucleus is undergoing mitosis, the protoplasmic connections between the cells of the carpogonial branch widen, and there is a movement of the cytoplasm along the branch into the carpogonium, possibly to furnish nourishment to this cell.

The communication between the carpogonium and the adjacent auxiliary cell is transient, simply furnishing a passage for the sporophytic nuclei into the pericentral cell. After their migration, the carpogonium becomes detached from the auxiliary cell and remains isolated for a while, without a nucleus, but finally breaks down with its three sister cells of the carpogonial branch.

The formation of the central cell and the development of the carpospores.—When the carpogonium becomes separated after its union with the auxiliary cell and the passage of its two sporophytic nuclei into the pericentral cell, all of the auxiliary cells become more closely united with one another. This condition takes place by the broadening of the protoplasmic communications that already exist between them. New communications are also established between neighboring auxiliary cells, so that the entire system becomes closely bound together by broad protoplasmic strands. These protoplasmic communications make possible the movement of the nuclei in the auxiliary cells towards the pericentral cell. This general cell union finally results in the formation of a large irregular cell, the central cell, as it was called by previous investigators (PHILLIPS **60**, and others), containing a number of nuclei. Two of these nuclei, as previously stated, are sporophytic and derived from the mitosis of the fusion nucleus in the fertilized carpogonium; the other nuclei, perhaps three or four in number, are gametophytic and derived from the auxiliary cells. The two sporophytic nuclei lie in the upper part of the central cell and the gametophytic nuclei below. There are not as many gametophytic nuclei in the large fusion cell as might be expected, because some of them have already broken down and the others generally show signs of disorganization.

The two nuclei of sporophytic origin give rise to a series of mitoses (*fig. 127*), and the central cell now develops several lobes, into each of which a single sporophytic nucleus generally passes (*fig. 128*). The nucleus contained within each lobe divides once more (*figs. 129, 130*) and a carpospore is cut off terminally (*fig. 131*) from the lobe by a cleavage furrow, the lower portion remaining as a stalk cell by which the carpospore is attached to the central cell (*fig. 132*).

The chromosomes appearing in the mitoses previous to the formation of the carpospore are clearly 40 in number. There is therefore no chromosome reduction at this period in the life history of Polysiphonia, for the sporophytic number 40 enters the carpospore and, as previously described, appears with the first mitosis at its germination. The period of chromosome reduction in Polysiphonia is at the time of tetraspore formation, as will be discussed presently. This is an important matter in relation to WOLFE'S (**86**) account of Nemalion, where he reports chromosome reduction as taking place just before the formation of the carpospores.

After the formation of the carpospores the central cell increases greatly in size, absorbing the stalk cells (*fig. 133*); and finally the cell of the axial siphon becomes involved in these extensive cell unions, which are probably concerned with the nourishment of the carpospores, since sixty or more, as a rule, are developed in a single cystocarp. While the carpospores are being formed, the characteristic envelop of the cystocarp becomes swollen and urn-shaped. This envelop is developed from the peripheral siphons of the procarpic branch; but is lined with a set of delicate filaments (*fig. 132, p f*), called paranematal filaments, that arise from the cell of the axial siphon.

Some of the gametophytic nuclei derived from the auxiliary cells break down before the unions or after the formation of the central cell. They swell greatly, the chromatin network becomes inconspicuous, the membrane grows thinner and finally dissolves, so that the nuclear contents mingle with the cytoplasm. Or, before the dissolution of the nuclear membrane, the network fades away, but large nucleolus-like globules appear, which after the breaking down of the membrane become distributed in the cytoplasm (*fig. 134*).

TETRASPORE FORMATION.

It is probable that true tetraspores are never formed on the sexual plants of Polysiphonia. Certain abnormalities will be discussed in the next section of this paper. The cell lineage of the tetraspore in the Rhodomelaceae was correctly described by FALKENBERG (**27**). HEYDRICH (**41**, **42**) gives an account in which he contends that the tetraspores are formed after a nuclear union within the mother cell, and that tetraspore formation may be the forerunner of a method of sexual reproduction. His studies seem to have been made upon unsatisfactory material and without cytological methods, to judge from his figures. Since I have not been able to confirm his conclusions or to establish any relation between them and my own, I shall not discuss them further.

The beginning of tetraspore formation is the development of a pericentral cell laterally from the central siphon (*fig. 140, pc*). The mitosis previous to the formation of the pericentral cell (*figs. 136–139*) shows that its nucleus contains 40 chromosomes. The pericentral cell then cuts off a cell above (*fig. 140, tmc*), which becomes the tetraspore mother cell, attached by a stalk (*fig. 140, sc*) to the central siphon.

The formation of the tetraspore mother cell was traced in detail through the prophase, metaphase, and anaphase of the nuclear division in the pericentral cell (*figs. 141–146*), and the number of chromosomes which enter the tetraspore mother cell is clearly 40.

Centrosphere-like structures also appear unmistakably at the metaphase of this mitosis (*fig. 142*), as well as in the previous mitosis (*fig. 137*).

The tetraspore mother cell (*fig. 147*) increases rapidly in size, soon becoming very much larger than the stalk cell. With the growth of the cell the nucleus also increases in size, and in the resting condition shows a conspicuous linin network. This network consists at first of lightly staining anastomosing threads, having knots here and there which stain a little darker (*figs. 147, 147a*). The cytoplasm presents a fine granular structure, with small alveoli. The nuclear network undergoes gradual change in such a manner that the lightly staining threads become somewhat thicker, and the knots grow into large irregular masses (*figs. 148, 148a*). Some portions of the threads connecting the knots become thinner and more slender, at last fading away; while other portions of them become thicker, and then the knots gradually diminish in bulk; so that, by and by, the anastomosing chromatin network becomes transformed into long continuous threads of irregular thickness, finally broadening into ribbons (*figs. 149, 149a*).

These chromatin threads or ribbons derived from the network now spread and become distributed throughout the nuclear cavity in a continuous and tangled fashion, presenting no free ends. It is difficult to decide whether there is a single continuous thread or a double structure, but probably the latter condition is present, for the threads generally run side by side in pairs (*figs. 150, 150a*). Most of the chromatin threads become more tangled, twisted, and massed at one side of the nuclear cavity, only a few traversing the cavity to the opposite side of the nuclear membrane. Synapsis is now generally believed not to be an artifact, and a careful study of this stage in Polysiphonia convinces me that the uniform chromatin threads which run parallel in pairs actually fuse into a single thread in certain portions, although at the same time they may be separated in other parts. All of this probably means that the two continuous threads resulting from the transformation of the chromatin network are of distinct origin, paternal and maternal, and that they come in contact where they run closely parallel, and finally fuse together in the tangled and contracted condition of synapsis, according to the recent interpretation of ALLEN (**1**, **2**, **3**, **4**), GRÉGOIRE (**35**), BERGHS (**7**, **8**, **9**, **10**), ROSENBERG (**64**, **65**, **66**), and others.

The period of synapsis lasts for some time, after which the spirem becomes looser and distributed throughout the nuclear cavity. This thread, at first uniform in thickness, begins to split longitudinally (*figs. 152, 152a*), the two parts lying close together side by side for long distances, but sometimes diverging at wide angles and then coming together again. The transverse segmentation of this double spirem to form the chromosomes now takes place, although not simultaneously throughout the entire nucleus. The shape of these chromosome segments is very irregular when first formed. They may be bent or twisted like two Vs (*fig. 153a, V*), or two Ls (*fig. 153a, L*) placed one above the other, or crossing in the form of an X (*fig. 153a, X*). The segments gradually shorten (*fig. 154*) until 20 short rod-shaped chromosomes, bivalent in nature, are formed (*fig. 155*). These are of course really the 40 sporophytic chromosomes now grouped in pairs. The nucleolus present in the resting nucleus of the tetraspore mother cell has not changed visibly up to this prophase stage, taking various positions, and during synapsis being surrounded by the tangled mass of threads. Thus the 40 chromosomes which entered the tetraspore mother cell now appear after synapsis, which is generally believed to be the period of chromosome reduction, as 20 pairs. These pairs become arranged in an equatorial plate and the chromosomes of the pairs split longitudinally, so that a large number of chromosomes results (*fig. 156*), probably 80 in all, but so crowded that it is not possible to count them with absolute certainty.

While these changes are taking place inside of the nucleus the kinoplasm accumulates in two opposite poles outside of the nuclear membrane. Each pole of the spindle which is formed (*fig. 156*) is occupied by a deeply staining centrosome-like body, as in the case of the prophase of the other mitoses previously described. The form of this spindle in the tetraspore mother cell is quite different from other mitoses. Its longest axis runs from pole to pole instead of across the equatorial plate, as in the other nuclear figures. Besides, the two poles are less than 180° apart, which gives an asymmetrical or somewhat bent form to the spindle when viewed from a certain direction, and also there are no clearly defined centrosphere-like structures.

The spindle of the first mitosis is of very short duration. As soon as the chromosomes at the equatorial plate separate into two groups, the two spindles of the second mitosis suddenly appear and the first spindle can no longer be recognized (*fig. 157*). It is possible that the two poles of the first spindle may move along the membrane and become poles of the second spindle, but I have no evidence to support this suggestion. Whatever the origin of the poles of the second mitosis, they are placed in an entirely different position from the poles of the first. The second mitosis in the tetraspore mother cell, therefore, follows so shortly after the first that there is no period between for the organization of two resting nuclei.

The rapidity with which the second mitosis follows the first may prevent the organization of centrosphere-like structures at the poles. The axis of the two spindles of the second mitosis lie perpendicular to each other (*figs. 157, 158*), and the two nuclear divisions take place simultaneously. At anaphase four groups of chromosomes, 20 in number, pass to the poles, still included in the membrane of original tetraspore mother cell, which persists from the beginning (*fig. 159*). These four groups, of 20 chromosomes each, contain all together the 80 granddaughter chromosomes shown in *fig. 156*. When the granddaughter chromosomes reach the four poles of the two spindles of the second mitosis, four masses of kinoplasm are present. The granddaughter chromosomes after reaching the poles soon begin to lose their individual outline, and become connected with one another to form a network (*fig. 160*). The original nuclear cavity contains at this stage a very large nucleolus-like body which appears during the anaphase of the second mitosis (*fig. 159*). The history of this body is not clear, but it seems to be a new structure, developing during the second mitosis, The four poles now begin to enlarge, while the region of the nuclear membrane between them becomes flattened (*fig. 160*); consequently the outline of the original nuclear membrane is somewhat tetrahedral at this stage. The transformation of the four groups of chromosomes into four chromatin nets proceeds until a chromatin reticulum occupies each of the four lobes of the original nuclear cavity.

The cytoplasm of the tetraspore mother cell has large alveoli, which pass into a finer structure at the periphery of the cell and at the nuclear membrane. This fine alveolar cytoplasm around the nucleus joins the kinoplasm, which lies directly against the nuclear membrane, at the four regions formerly occupied by the poles of the spindles of the second mitosis (*fig. 160*). These kinoplasmic masses extend along the membrane between the four lobes. Finally the membrane breaks down between the lobes and the kinoplasm enters the nuclear cavity in the form of fibrils (*fig. 161*), which grow slowly towards the center, where they finally meet around the nucleolus-like body which now shows signs of fragmentation. The four groups of daughter chromosomes, passing into a chromatin network, thus become surrounded by kinoplasm (*fig. 162*) and separated from one another as four daughter nuclei (*figs. 163, 163a*). During this process the nuceolus-like body, formerly occupying the center of the nuclear cavity, fragments into four or more portions, which become distributed to the four daughter nuclei.

The daughter nuclei and the tetraspore mother cell continue their growth after nuclear division, these four nuclei remaining closely associated with one another for a long while (*fig. 165*). Cleavage furrows have begun to form at the periphery of the cell a little before or after the end of nuclear division. The arrangement of these furrows may be compared to the six edges of four spherical tetrahedrons whose apices are pointed towards the center of the tetraspore mother cell. The cleavage furrows slowly grow inward (*figs. 165, 165a*), and finally meet at the center of the mother cell between the four daughter nuclei, thus dividing the protoplast into tetraspores. The mechanism of the cell division by cleavage furrows is similar to that of the vegetative cells, *i. e.*, the furrow is assisted in its growth inward by the fusion of the small vacuoles.

Throughout the whole process of tetraspore formation the mother cell remains connected with the stalk cell by a strand of protoplasm, and probably obtains nourishment through this strand, since the developing tetraspores increase greatly in size.

ABNORMALITIES.

Normally the male and female organs and tetraspores are found on three different individuals, but it often happens that antheridia and procarps are produced by the same plant. Sperms are occasionally developed in clusters at the nodal regions of older portions of filaments, more often on male plants, but sometimes they are formed near the base of cystocarps. The sexual cells in these cases develop normally, the successive mitoses showing 20 chromosomes.

Frequently certain of the stalk cells in an antheridium increase greatly in size (*fig. 166*) and divide again and again (*fig. 167*). The cytoplasmic structure and behavior of the cells resemble somewhat the auxiliary cells of the procarp, and it seems possible that there is present in such cases an organ of somewhat mixed character.

The most noteworthy abnormalities, however, are those where cystocarpic or antheridial plants produce cells whose lineage is identical with that of the tetraspore mother cell (*figs. 168–170g*). The development of these cells was traced until they reached their full size (*figs. 170a–170g*), yet the nuclei in almost all cases remained undivided (*fig. 170d′*), although the beginnings of cleavage furrows were observed as shallow grooves (*figs. 169–170g*). These cleavage furrows never proceeded to the interior of the cell. Very rarely the nucleus appeared to enter a mitosis (*figs. 171, 171a, 171a′*) in old cells, but the number of chromosomes, small and round, were about 20 in each daughter group, and there was no evidence of reduction phenomena; indeed, the cell was never divided. Whether this cell may escape from the parent plant and germinate as a monospore has not yet been determined.

It seems probable that this peculiar behavior in Polysiphonia may offer an explanation of similar cases reported in the red algae where tetraspores are formed on sexual plants. They have been noted in *Chylocladia kaliformis* (LOTSY **45**), *Spermothamnion Turneri* and *Ceramium rubrum* (DAVIS **24**), and DAVIS has also observed them on *Callithamnion Baileyi*. Such cases should be carefully investigated to determine whether true tetraspores are present or whether the structures are not really of the nature of monospores, as in Polysiphonia, and developed with a suppression of reduction phenomena. In this case the apparent irregularity of the presence of asexual spores on a sexual plant would be explained; or it is of course possible that in some cases the tetraspores are formed normally, but the sexual organs are developed apogamously. However, it seems more probable that the first alternative will be found to be the explanation of these exceptional conditions in the red algae.

DISCUSSION OF CYTOLOGICAL PHENOMENA.

The nucleolus.—The morphology of the nucleolus and its behavior and function during mitoses have been studied in some detail for two decades by many investigators in both plant and animal cells. Various conclusions have been reached by different authors for the various forms examined, and the same author has not unfrequently changed his view when he came to study different material. From the excellent comparative studies of MONTGOMERY (**48**) and work done later, it is possible to summarize the essentials of the most important views as follows.

ZACHARIAS (**88**) proposed the theory that the nucleolus contains no chromatin, after FLEMMING'S conclusion (**33**) that there were chemical differences between true nucleoli and the chromatin reticulum. This view has been followed by various authors, who have concluded that there is no relation between the formation of chromosomes and the disappearance of nucleoli. This seems to be the condition in Polysiphonia.

STRASBURGER (**72, 74**) published the view that the substance of the nucleolus is utilized for spindle formation, which conclusion was drawn from the fact that the nucleolus in many forms disappears partly or completely, immediately preceding the formation of the spindle. Later NĚMEC (**54**) suggested that the disappearance of the nucleolus and the formation of the spindle may be regarded as two independent events, which take place simultaneously. STRASBURGER'S view has been followed by FAIRCHILD (**26**), HARPER (**38**), WILLIAMS (**81**), and others. The spindle formation of Polysiphonia will be considered in the next section under the heading "spindle formation."

STRASBURGER (**70**), however, formerly held the view that the nucleolus was reserve material serving to build up the chromosomes. This theory has been followed by PFITZNER (**59**), GUIGNARD (**37**), FARMER (**29, 30**), SARGANT (**67**), SWINGLE (**76**), CARNOY and LEBRUN (**13**), CHAMBERLAIN (**15, 16**), DUGGAR (**25**), ANDREWS (**5**), MOTTIER (**52**), CAVARA (**14**), WAGER (**80**), and others.

Some authors have gone still further and concluded that the chromosomes in certain forms are formed directly from the nucleolus. The studies of the algae and of lower unicellular organisms seem to support this conclusion. Thus TANGL (**77**), MEUNIER (**46**), MOLL (**49**), DECAGNY (**24***a*), HENNEGUY (**40**), MITZKEWITSCH (**47**), and VAN WISSELINGH (**83**, **84**) on Spirogyra, GOLENKIN (**34**) on Sphaeroplea, and WOLFE (**86**) on Nemalion hold this view. There are naturally some differences in details among the authors mentioned above. For example, MOLL states that the nucleolus of Spirogyra is found commonly exhibiting a skein structure, and that segments are formed by the transference of chromatin substance from the nucleolus into a nuclear plasm as small fragments arranged like beads in a necklace. MITZKEWITSCH points out that during mitosis the nucleolus increases in size and becomes differentiated into a number of deeply staining granular chromosomes. VAN WISSELINGH believes that in the same genus only two out of the eight chromosomes are derived from the nucleolus, and that in the reorganization of daughter nuclei both halves of these two chromosomes give rise to the new nucleoli. GOLENKIN describes the nucleolus of Sphaeroplea as breaking up into a number of chromosomes which become arranged in a nuclear plate. WOLFE on Nemalion states that the material of the nucleolus passes outward through radiating fibrillae (linin ?) into a number of chromatin granules, which organize the chromosomes directly without the intervention of a spirem stage.

The most recent study on Spirogyra is by BERGHS (**11**). He concludes that the nuclear network is not of chromatin nature, at least it contains in the resting state little chromatin and does not take part in the formation of chromosomes, whereas the nucleolus, at least at prophase, contains all of the chromatin elements and does not disappear at any moment of mitosis. The nucleolus consists of two substances; from the first, 12 chromosomes become differentiated and arranged in a ring at the equatorial zone; the second substance remains in the form of the original nucleolus. The second substance at anaphase splits into two groups of small rods ("bâtonnets"), forming segments which pass to the poles with the chromosomes. These segments are 6 in number, but are double longitudinally. The true chromosomes become attached in pairs at the equatorial ends of these segments.

The daughter nucleoli are reconstructed at the expense of the double segments. These undergo an active vacuolization and are then condensed into a nucleolus in which the two substance are again mixed together.

According to other views, there may be more than one kind of structure called a nucleolus. CARNOY (**12***a*) makes four groups of these structures as follows: *nucléolus nucléinieus, nucléolus noyaux, nucléolus plasmatiques*, and *nucléolus mixtes*, the first one being considered as portion of the chromatin network and the third concerned with the formation of the spindle. Other authors (ROSEN **62**, DAVIS **22**, WILSON **82**) have recognized two kinds of nucleoli, true nucleoli and chromatin nucleoli, the latter being considered entirely of chromatin.

In Polysiphonia the nucleolus lies in various positions within the nuclear cavity, and is not connected with the chromatin network. The chromosomes are formed from the gradual transformation or rearrangement of the substance of the network, and the nucleolus takes no part in their development. In Corallina also DAVIS (**18**) clearly distinguishes the chromatin bodies from the nucleolus.

Spindle formation.—The spindle fibers in Polysiphonia are meagerly developed and of short duration. During the prophase of mitosis the nucleolus remains unchanged and the two poles are marked by deeply staining bodies, but I regret that I have not been able to trace the process of spindle formation. In the sporelings, where the nucleus is comparatively large in size and the spindles are more conspicuous, it was noted that short slender fibrils are attached to the chromosomes when assembled irregularly in the middle region of the nuclear cavity (*figs. 3, 17*). These fibrils are the remains of the nuclear network and are the only fibrillar structures ever seen within the nuclear membrane at this time. The centrosome-like bodies, which at metaphase seem to become the centers of the well-differentiated centrosphere-like structures, have no radiation into the cytoplasm, though in the case of sperm mother cells a few fibrillae may be seen running from the centrosome-like bodies at prophase (*fig. 64*). I have not observed the entrance of spindle fibers from the kinoplasmic centers outside of the nucleus, as has been reported by DAVIS (**18**) for Corallina.

Harper (**39**) states that, after the synaptic stage in the ascus of Phyllactinia, a number of strands of chromatin are attached to a central body, and that each strand corresponds to a single chromosome. He shows that the resting nucleus of Phyllactinia has definite polarity. The formation of chromosomes from a strand of the spirem consists in the segregation of two substances present in the spirem. The densely staining chromatin aggregates into chromosomes, leaving the achromatic portion as a series of threads connecting the chromosomes to the central body, and these threads later form the spindle. I have studied Polysiphonia very carefully in the hope of relating its process of spindle formation to that of Phyllactinia, but have not been able to find any essential resemblance. There seems to be no polarity to the resting nucleus of Polysiphonia as described by **Harper** for Phyllactinia.

Centrosome and centrosphere-like structures.—Every mitosis, no matter where it occurs, is characterized by the constant presence during prophase of two sharply differentiated centrosome-like bodies in the center of the kinoplasm at opposite ends of the nucleus. When the chromosomes are arranged in the equatorial plate the kinoplasm has the form of a large centrosphere-like structure at the pole of the spindle, and the centrosome-like bodies have disappeared. These structures are destitute of the astral rays, characteristically accompanying typical centrosomes or centrospheres, as reported in Fucus (**Strasburger 73**, **Farmer** and **Williams 32**), Stypocaulon (**Swingle 76**), Dictyota (**Mottier 52**, **Williams 81**), and in animal cells. They have a compact, homogeneous structure in Polysiphonia, which makes them readily distinguishable from the surrounding protoplasm. The daughter chromosomes, after their separation at the equatorial plate, become gathered close to each centrosphere-like structure at anaphase of mitosis, and in contact with it. The latter then passes into a vague kinoplasmic mass which surrounds the group of daughter chromosomes.

The observations summarized above, namely the appearance of a centrosome-like body at prophase, its progressive development and differentiation as a large centrosphere-like structure during metaphase, which is the climax of the kinoplasmic activity of mitosis, and its gradual decline after anaphase, lead me to conclude that these structures in Polysiphonia are not permanent organs of the cell, but are formed *de novo* with each mitosis, to carry on the mechanism of nuclear division.

HARPER (**39**) has published an important discussion on a "central body" discovered by him in Phyllactinia. In this form the central body lies within the membrane of the resting nucleus, and is connected with chromatic strands so as to give polarity to the nucleus. The poles of the spindles are formed by division of the central body. HARPER believes in the permanence of this structure, from mitosis to mitosis, and in the maintenance of its connection with the chromatin. The permanent nature of the central body in Phyllactinia and the transient appearance of centrosphere-like structures in Polysiphonia seem at present difficult of reconciliation.

In Nemalion WOLFE (**86**) reports that centrosomes are present without astral rays at metaphase, but their continuity was not established. The centrosphere described by DAVIS (**18**) in the tetraspore mother cell of Corallina is formed *de novo* in each mitosis. Their transient nature agrees with the somewhat similar structures of Polysiphonia.

The reduction of chromosomes.—STRASBURGER'S paper (**71**) entitled "The periodic reduction of the number of chromosomes in the life history of the living organisms" was the first presentation of the significance of sporogenesis and reduction phenomena in relation to alternation of generations in plants. His conclusions were based upon the discoveries that nuclei in the sporophyte generations of higher plants have double the number of chromosomes found in the nuclei of the gametophyte generations, and that the reduction of this double number takes place at the period of sporogenesis. This theory has been well established so far as groups of plants above the thallophytes are concerned, and the period of chromosome reduction has been found to be always associated with sporogenesis, and never with gametogenesis as in the case of animals. However, among the thallophytes our actual knowledge of facts concerning the reduction period is meager.

Suggestions of the presence of reduction phenomena at gametogenesis have been made among the fungi in the Peronosporales (ROSENBERG **63**) and Saprolegniales (TROW **79**). ROSENBERG describes what he has called a synaptic stage in the nucleus preceding the two mitoses concerned with oogensis in Plasmopara, and TROW holds that chromosome reduction takes place in the two mitoses in the oogonium of Achyla. These interpretations have been discussed and criticized by DAVIS (**21**, **23**), and the suggestions of ROSENBERG and TROW do not seem to me convincing.

Among algae, one of the best known accounts of gametogenesis is that of Fucus (STRASBURGER **73**, FARMER and WILLIAMS **32**), where, although spermatogenesis has not been investigated, the history of oogenesis indicates a period of chromosome reduction. Consequently the fusion nucleus in the fertilized egg has the same number of chromosomes as the nucleus in the vegetative plants of Fucus, which led STRASBURGER (**73**, **75**) to conclude that the Fucus plant is a sporophyte generation and that the gametophyte is so greatly reduced that it is only represented by single cells —male and female gametes —before fertilization.

Other examples among the thallophytes in which the life history has been worked out in some detail are Dictyota and Nemalion. In Dictyota (WILLIAMS **81**) the fertilized egg nucleus gives rise to an asexual plant with double the number of chromosomes, and consequently a sporophytic generation. This asexual plant develops spores in groups of four accompanied by chromosome reduction, and these spores develop the gametophyte generation. This type of life history is clearly analogous to that of Polysiphonia. In Nemalion (WOLFE **86**) the fusion nucleus of the fertilized carpogonium has a double number of chromosomes which appear in all of the cells of the cystocarp (sporophytic) up to the formation of carpospores, where the reduced number of the gametophyte is reported to appear. WOLFE's account, however, does not give the details of this chromosome reduction with the characteristic stage of synapsis followed by two successive mitoses.

Chromosome reduction in Polysiphonia is clearly similar to the phenomena of sporogenesis in higher plants, and takes place at the time of tetraspore formation. The carpospores, containing the sporophytic number of chromosomes, continue the sporophyte generation by developing the tetrasporic plant. The appearance of synapsis just previous to the formation of the tetraspores, followed by two successive mitoses with their peculiar distribution of the chromosomes, is similar in all essentials to the reduction division in the higher plants and in Dictyota.

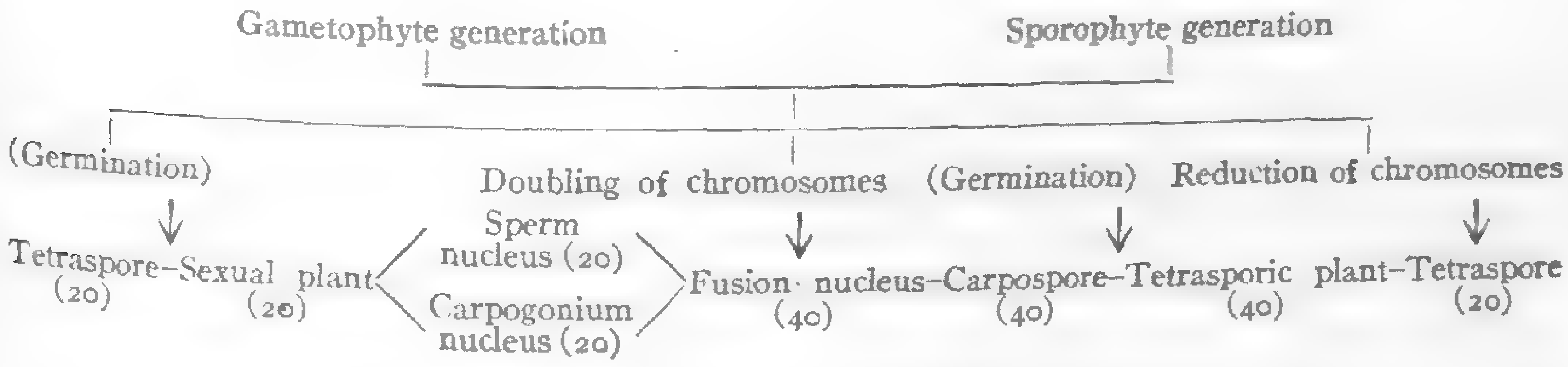
The mitoses in the tetraspore mother cell have certain peculiarities that deserve special consideration. The first mitosis is followed so rapidly by the second that there are no resting nuclei organized between the two divisions. In this respect the history of sporogenesis resembles that of Pallavicinia reported by MOORE (**50**, **51**), but there is this difference, that in Polysiphonia the granddaughter chromosomes present in the second mitosis are formed before the first and within the original membrane, and the organization of the four granddaughter nuclei takes place simultaneously. However, the distribution of the granddaughter chromosomes is clearly effected through two mitoses and two sets of spindles, so there is never present a quadripolar spindle such as was described by FARMER (**28**, **29**, **30**, **31**) for Pallavicinia and some other forms of Hepaticae, and has been called in question by DAVIS (**19**) and MOORE (**50**, **51**).

ALTERNATION OF GENERATIONS.

Alternation of generations.—Judging from the studies of Polysiphonia presented above, the male and female plants with their 20 chromosomes are gametophytes. The union of the male and female nuclei results in the fertilized carpogonium with the double number of chromosomes (40), marking the beginning of a new phase, the sporophyte generation. This fusion nucleus gives rise to a series of mitoses in the central cell of the cystocarp, all characterized by the double number of chromosomes, and consequently sporophytic in character, and carpospores are finally formed. The carpospore on germination presents the same number of chromosomes (40), and the successive mitoses following contain this number, so that the sporeling developed from the carpospore is still a part of the sporophytic phase. It may never be possible to grow such sporelings to maturity under experimental conditions, but it is evident that the plant developed from the carpospore must have nuclei with 40 chromosomes, until there is some marked change in the life history. The only vegetative form of Polysiphonia with 40 chromosomes is the tetrasporic plant, from which it must be inferred that the tetrasporic plant arises from the carpospore and constitutes a part of the sporophyte generation that begins with the fertilized carpogonium .

This long sporophytic phase terminates with the formation of tetraspores, when a reduction of chromosomes takes place, 20 chromosomes entering each tetraspore. These tetraspores with the reduced number of chromosomes evidently have returned, with respect to nuclear conditions, to the potentialities of the original gametophyte or sexual generation. Again, it may never be possible to grow sporelings from the tetraspore to maturity under experimental conditions, but it is evident that plants derived from the tetraspores must have nuclei with 20 chromosomes. The sexual plants of Polysiphonia are the only forms in which 20 chromosomes are found, therefore it may safely be concluded that the sexual plants arise from tetraspores. The tetraspore then constitutes an indispensable part of the life history of Polysiphonia, and cannot be regarded simply as an accessory type of reproductive structure, such as is illustrated by many forms of asexual spores in the thallophytes or by the gemmae of bryophytes.

To summarize the life history of Polysiphonia, the gametophyte generation begins with the tetraspores and ends with the sexual cells or gametes, whose fusion initiates the sporophyte generation; this covers a long period, including the formation of carpospores, germination of carpospores, development of the tetrasporic plants, and at last ends with the formation of tetraspores. In other words, the sexual plants and the tetrasporic plants present the two distinct phases of an antithetic alternation of generations, with the cystocarp a part of the sporophytic phase, The life history of Polysiphonia may be tabulated as follows:



Taking up the theories concerning the life history of the red algae, OLTMANNS (**55**) concluded eight years ago, from an investigation of four genera (Dudresnaya, Gloeosiphonia, Callithamnion, and Dasya), that the structure derived from the fertilized carpogonium is comparable to the sporophyte generation of the higher plants. At that time he expressed his opinion definitely that the tetraspore is a special form of reproductive cell, comparable to brood cells or gemmae, and with no fixed place in the life history. However, during the last year (**56**, p. 273) he has admitted the possibilities of reduction phenomena during tetraspore formation.

DAVIS (**24**, pp. 467, 471) in the same year definitely suggested the probability that reduction phenomena would be found in the tetraspore mother cell.

WILLIAMS (**81**) discovered chromosome reduction during tetraspore formation in Dictyota, which led him to conclude that the tetrasporic plant in Dictyotaceae is a sporophyte generation derived from the fertilized egg.

WOLFE (**86**) showed for Nemalion that the cells of the cystocarp have double the number of chromosomes found in the sexual plant, thus presenting the first cytological evidence that the cystocarp of the red algae is sporophytic in character. He places the period of chromosome reduction at the time of carpospore formation, basing his conclusion on a count of chromosomes in the mitosis just previous to the formation of the carpospores. However, he did not report the phenomena characteristic of chromosome reduction, namely the period of synapsis followed by the two mitoses which distribute the chromosomes so as to give a numerical reduction.

Recently STRASBURGER (**75**) has published his views concerning the alternation of generations in the brown algae, remarking that the tetraspores of the red algae seem to be different from those of the Dictyotaceae, and that the place of the chromosome reduction in the red algae should be sought elsewhere than at tetraspore formation, because some of the red algae develop no tetraspores, but instead form monospores. It is true that in some groups of red algae tetraspores are never formed, and in certain of these monospores are present. In these cases chromosome reduction may take place with the formation of the carpospores, or perhaps with their germination, and the monospore when present may have no vital relation to the main cycle of the life history. The group of the red algae is very large and contains a great variety of forms, with a wide range in the complexity of the cystocarp and the vegetative forms, so that it is reasonable to expect important differences in the position of the period of chromosome reduction.

Origin of the tetraspore.—The simplest genera of the red algae, such as Lemanea, Batrachospermum, Chantransia, and Nemalion, have no tetraspores, but some of them have monospores, as in Chantransia and Batrachospermum (including the Chantransia form). In these types the period of chromosome reduction may be associated with the carpospore, either just before its development or at the time of its germination. The monospores, then, in such genera are not vitally concerned with the life history, and indeed are present upon the gametophyte. The tetrasporic plant may have arisen by a suppression of the reduction phenomena in connection with the carpospore, so that it germinates with the sporophytic number of chromosomes, producing a plant with this number, which consequently becomes at once a part of the sporophytic phase. The period of chromosome reduction would be thus postponed from the carpospore to a later period in connection with the newly formed plant. Such plants by developing tetraspores would end the sporophyte generation. It is quite possible that the first tetraspore mother cells corresponded to monospores on the sexual plants except that they had the double number of chromosomes, since such reproductive cells would very naturally become the seat of the delayed reduction phenomena. The resemblance in general morphology of the tetrasporic plants in the red algae to the sexual plants would be expected, because they live under similar environmental conditions, and we have another illustration of such similarity of gametophytes and sporophytes in the Dictyotaceae.

Abnormalities of the nature of monospores.—It should be remembered that sexual plants (cystocarpic) of Polysiphonia occasionally develop an abnormality in the form of a cell resembling a monospore but having the same cell lineage as the tetraspore mother cell. This abnormality may indeed be a reversion to an ancestral type of monospore, that in the process of evolution has given place to the tetraspore mother cell, which is only found in the sporophytic generation. It may be, however, simply an exceptional condition without any phylogenetic significance.

SUMMARY.

The nuclear conditions in the life history of *Polysiphonia violacea* may be summarized as follows:

1. The carpospore on germination shows 40 chromosomes, and 40 chromosomes appear in the vegetative mitoses of the tetrasporic plant; so it may be inferred that the tetrasporic plants come from carpospores.

2. The tetraspore on germination shows 20 chromosomes, and 20 chromosomes appear in the vegetative mitoses of the sexual plant; so it may be inferred that the sexual plants come from tetraspores.

3. The nuclei of the gametes (sperm and carpogonium) contain each 20 chromosomes. The fusion nucleus (sporophytic) in the fertilized carpogonium as a result has 40 chromosomes and gives rise to a series of nuclei in the central cell. Some of these enter the carpospores, which are consequently a part of the sporophytic phase to be continued in the tetrasporic plant. The gametophyte nuclei in the central cell of the cystocarp with 20 chromosomes break down.

4. Tetraspore formation terminates the sporophytic phase with typical reduction phenomena, so that the tetraspores are prepared to develop the gametophyte generation.

5. There is thus an alternation of a sexual plant (gametophyte) with a tetrasporic plant (sporophyte) in the life history of Polysiphonia, the cystocarp being included as an early part of the sporophytic phase.

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LITERATURE CITED.

1. ALLEN, CHARLES E., Chromosome reduction in *Lilium canadense.* BOT. GAZETTE **37**:464. 1904.
2. ———, Nuclear division in the pollen mother cell of *Lilium canadense.* Annals of Botany **19**:189. 1905.
3. ———, Das Verhalten der Kernsubstanzen während der Synapsis in den Pollenmutterzellen von *Lilium canadense.* Jahrb. Wiss. Bot. **42**:71. 1905.
4. ———, Die Keimung der Zygote bei Coleochaete. Ber. Deutsch. Bot. Gesells. **33**:286. 1905.
5. ANDREWS, FRANK M., Karyokinesis in Magnolia and Liriodendron, with special reference to the behavior of the chromosomes. Beih. Bot. Centralb. **11**:134. 1901.
6. BAUER, E., Zur Frage nach der Sexualität der Collemaceen. Ber. Deutsch. Bot. Gesells. **16**:363. 1898.

7. Berghs, Jules, Formation des chromosomes hétérotypiques dans la sporogénèse végétale. I. Depuis le spirème jusqu'aux chromosomes mûrs dans la microsporogénèse d' *Allium fistulosum* et de *Lilium lancifolium* (*speciosum*). La Cellule **21**:173. 1904.
8. ———, II. Depuis la sporogonie jusqu'au spirème définitif, dans la microsporrogénèse de l' *Allium fistulosum.* La Cellule **21**:383. 1904.
9. ———, III. La microsporogénèse de *Convallaria majalis.* La Cellule **22**:43. 1905.
10. ———, IV. La microsporogénèse de *Drosera rotundifolia*, *Narthecium ossifragum*, et *Helleborus foetidus.* La Cellule **22**:141. 1905.
11. ———, Le noyau et la cinèse chez le Spirogyra. La Cellule **23**:55. 1906.
12. Bornet et Thuret, Recherches sur la fécondation des Floridées. Ann. Sci. Nat. Bot. V. **7**:137. 1867.
12*a*. Carnoy, J. B., La cytodiérèse chez les Arthropodes. La Cellule **1**:191. 1885.
13. Carnoy and Lebrun, La cytodiérèse de l'œuf. La vésicule germinative et les globules polaires chez les Batraciens. La Cellule 189. **12**: 1897 and **14**: 109. 1898.
14. Cavara, F., Breve contribuzione alla conoscenza del nucleole. (Bollettino della Società Botanica Italiana **5–6**: 1902). Rev. in Bot. Centralb. **90**:338. 1902.
15. Chamberlain, Charles J., Oogenesis in *Pinus Laricio.* Bot. Gazette **27**: 268. 1899.
16. ———, Mitoses in Pellia. Bot. Gazette **36**:28. 1900.
16*a*. Darbishire, O. V., Ueber die Apothecienentwickelung der Flechte *Physcia pulverulenta* (Schreb.) Nyl. Jahrb. Wiss. Bot. **34**:329. 1899.
17. Davis, Bradley M., The fertilization of Batrachospermum. Annals of Botany **10**:49. 1896.
18. ———, Kerntheilung in der Tetrasporemutterzellen bei *Corallina officinalis* L. var. *mediterranea.* Ber. Deutsch. Bot. Gesells. **14**:266. 1898.
19. ———, Nuclear studies on Pellia. Annals of Botany **15**:147. 1901.
20 ———, The origin of the sporophyte. Amer. Nat. **37**:411. 1903.
21. ———, Note on Rosenberg's "Ueber den Befruchtung von Plasmopara." Bot. Gazette **36**:154. 1903.
22. ———Studies on the plant cell. I. Amer. Nat. **38**:367. 1904.
23. ———, Fertilization in the Saprolegniales. Bot. Gazette **39**:61. 1905.
24. ———, Studies on the plant cell. VI. Amer. Nat. **39**:449. 1905.
24*a*. Decagny, Ch., Recherches sur la division du noyau cellulaire chez les végétaux. Bull. Soc. Bot. France **42**:319. 1895.
25. Duggar, B. M., On the development of the pollen grain and embryo sac in *Bignonia venusta.* Bull. Torr. Bot. Club **26**:89. 1899.
26. Fairchild, D. G., Ueber Kerntheilung und Befruchtung bei *Basidiobolus ranarum* Eidam. Jahrb. Wiss. Bot. **30**:283. 1897.
27. Falkenberg, P., Die Rhodomelaceen des Golfes von Neapel und der

angrenzenden Meeresabschnitte. Fauna und Flora des Golfes von Neapel **26** Monographie. Berlin. 1901.

28. FARMER, J. B., Studies in Hepaticae: On *Pallavicinia decipiens* Mitten. Annals of Botany **8**:35. 1894.
29. ———, Spore formation and karyokinesis in Hepaticae. Annals of Botany **9**:363. 1895.
30. ———, On spore formation and nuclear division in the Hepaticae. Annals of Botany **9**:469. 1895.
31. ———, The quadripolar spindle in the spore mother cell of *Pellia epiphylla*. Annals of Botany **15**:431. 1901.
32. FARMER, J. BRETLAND, and WILLIAMS, J. LLOYD, Contribution to our knowledge of the Fucaceae; their life history and cytology. Phil. Trans. Roy. Soc. London B. **190**: 623. 1898.
33. FLEMMING, W., Zellsubstanz, Kern und Zellteilung. Leipzig. 1882.
34. GOLENKIN, M., Fertilization of *Sphaeroplea annulina*. (Bull. Soc. Imp. Nat. Moscou **1899**:343) Rev. in J. R. M. S. **1901**:65.
35. GRÉGOIRE, VICTOR, La réduction numérique des chromosomes et les cinèse de maturation. La Cellule **21**:297. 1904.
36. GRÉGOIRE, VICTOR, and WYGAERTS, A., La réconstitution du noyau et la formation des chromosomes dans les cinèses somatiques. I. Racine de *Trillium grandiflorum* et télophase homoeotypique dans le *Trillium cernuum*. La Cellule **21**:7. 1904.
37. GUIGNARD, L., Nouvelles recherches sur le noyau cellulaire, etc. Ann. Sci. Nat. Bot. VI. **20**:310. 1885.
38. HARPER, R. A., Kerntheilung und freie Zellbildung im Ascus. Jahrb. Wiss. Bot. **30**:247. 1899.
39. ———, Sexual reproduction and the organization of the nucleus in certain mildews (Phyllactinia). Carnegie Institution, Washington. 1905.
40. HENNEGUY, L. F., Leçons sur la cellule. Paris. 1896.
41. HEYDRICH, F., Die Befruchtung des Tetrasporangium von *Polysiphonia violacea* Greville. Ber. Deutsch. Bot. Gesells. **19**:55. 1901.
42. ———, Das Tetrasporangium der Florideen ein Vorläufer der sexuellen Fortpflanzung. Bibliotheca Botanica Heft 57. Stuttgart. 1902.
43. JANCZEWSKI, D., Notes sur le développement du cystocarpe dans les Floridées. Mém. Soc. Nat. Cherbourg **20**:109. 1877.
44. LAWSON, ANSTRUTHER A., On the relationship of the nuclear membrane to the protoplast. BOT. GAZETTE **35**:305. 1903.
45. LOTSY, J. P., Die Wendung der Dyaden beim Reifen der Tiereier als Stütze für die Bivalenz der Chromosomen nach der numerischen Reduktion. Flora **93**:65. 1904.
46. MEUNIER, A., Le nucléole des Spirogyra. La Cellule **3**:333. 1888.
47. MITZKEWITSCH, Ueber die Kerntheilung bei Spirogyra. Flora **85**:81. 1898.
48. MONTGOMERY, TH. H., Comparative cytological studies, with especial regard to the morphology of the nucleolus. Journal of Morphology **15**:625. 1899.

49. Moll, J. W., Observations on karyokinesis in Spirogyra. Verh. Kon. Akad. Amsterdam **9**:—. 1893.

50. Moore, Andrew C., The mitosis in the spore mother cell of Pallavicinia. Bot. Gazette **36**:384. 1903.

51. ———, Sporogenesis in *Pallavicinia*. Bot. Gazette **40**:81. 1905.

52. Mottier, D. M., Nuclear and cell division in *Dictyota dichotoma*. Annals of Botany **14**:163. 1900.

53. ———, Fecundation in plants. Carnegie Institution. Washington. 1904.

54. Němec, B., Neue cytologische Untersuchungen. Fünfstück's Beiträge zur wissenschaftliche Bot. **4**: 37. 1900.

55. Oltmanns, F., Zur Entwickelungsgeschichte der Florideen. Bot. Zeit. **56**:99. 1898.

56. ———, Morphologie und Biologie der Algen **2**. Jena. 1905.

57. Osterhout, W. J. V., Befruchtung bei Batrachospermum. Flora **87**:109. 1900.

58. Overton, James B., Ueber Reduktionstheilung in den Pollenmutterzellen einiger Dikotylen. Jahrb. Wiss. Bot. **42**:121. 1905.

59. Pfitzner, W., Beiträge zur Lehre vom Bau des Zellkerns und seinen Theilungs-Erscheinungen. Arch. Mikr. Anat. **22**: 616. 1883.

60. Phillips, R. W., On the development of the cystocarp in Rhodomelaceae. Annals of Botany **9**:289. 1895.

61 ———, On the development of the cystocarp in Rhodomelaceæ. Annals of Botany **10**:185. 1896.

62. Rosen, F. von, Beiträge zur Kenntniss der Pflanzenzellen. Cohn's Beitr. Biol. Pflanzen **5**:443. 1892.

63. Rosenberg, O., Ueber die Befruchtung von *Plasmopara alpina* (Johans). Beihang K. Svenska Vet.-Akad. Handl. **28**:—. 1903.

64. ———, Ueber die Tetradenteilung eines Drosera-Bastardes. Ber. Deutsch. Bot. Gesells. **22**:47. 1904.

65. ———, Ueber die Reduktionsteilung in Drosera. Meddel. Stock Hogs. Bot. Inst. 1904.

66. ———, Zur Kenntniss der Reduktionsteilung in Pflanzen. Bot. Notis. **1905**: 1–24.

67. Sargant, Ethel, Direct nuclear division in the embryo-sac of *Lilium Martagon*. Annals of Botany **10**: 107. 1896.— The formation of the sexual nuclei in *Lilium Martagon*. Ibid. **11**: 187. 1897.

68. Schmidle, W., Einiger über die Befruchtung, Keimung u. Haarinsertion von Batrachospermum. Bot. Zeit. **57**:125. 1899.

69. Schmitz, Fr., Untersuchungen über die Befruchtung der Florideen. Sitz. Kön. Akad. Wiss. Berlin. 1883.

70. Strasburger, Ed., Ueber den Theilungsvorgang der Zellkern u. das Verhaltniss der Kerntheilung zur Zelltheilung. Arch. Mikr. Anat. **21**: 476. 1882

71. STRASBURGER, ED., Periodic reduction of the number of chromosomes in the life history of living organisms. Annals of Botany **8**:281. 1894.

72. ———, Karyokinetische Probleme. Jahrb. Wiss. Bot. **28**:151. 1895.

73. ———, Kerntheilung und Befruchtung bei Fucus. Jahrb. Wiss. Bot. **30**: 351. 1897.

74. ———, Ueber Reduktionsteilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich. Histol. Beitr. **6**. 1900.

75. ———, Zur Frage eines Generationswechsel bei Phaeophyceen. Bot. Zeit. **64**:2. 1906.

76. SWINGLE, W. T., Zur Kenntniss der Kern- und Zelltheilung bei den Sphacelariaceen. Jahrb. Wiss. Bot. **30**:297. 1897.

77. TANGL, E., Ueber die Theilung der Kerne in Spirogyra-Zellen. Sitz. Akad. Wiss. Wien **85**:628. 1882.

78. THAXTER, R., Contribution towards a monograph of the Laboulbeniaceae. Mem. Amer. Acad. **12**. 1896.

79. TROW, A. H., On fertilization in the Saprolegnieae. Annals of Botany **18**:541. 1904.

80. WAGER, HAROLD, The nucleolus and nuclear division in the root apex of Phaseolus. Annals of Botany **18**:29. 1904.

81. WILLIAMS, J. LLOYD, Studies in the Dictyotaceae. I. Cytology of the tetraspore and germinating tetraspore. Annals of Botany **18**:143. 1904. II. Cytology of the gametophyte. Annals of Botany **18** : 181. 1904.

82. WILSON, E. B., The cell in development and inheritance. New York. 1904.

83. VAN WISSELINGH, Ueber den Nucleolus von Spirogyra. Bot. Zeit. **55**:195. 1898.

84. ———, Ueber Kerntheilung bei Spirogyra. Flora **87**:378. 1900.

85.———, Untersuchungen über Spirogyra. Bot. Zeit. **60**:115. 1902.

86. WOLFE, J. J., Cytological studies in Nemalion. Annals of Botany **18**:608. 1904.

87. YAMANOUCHI, S., The life history of *Polysiphonia violacea* Grev. (Preliminary note.) BOT. GAZETTE **41**:425. 1906.

88. ZACHARIAS, E., Ueber den Nucleolus. Bot. Zeit. **43**:257, 273, 289. 1885.

EXPLANATION OF PLATES XIX–XXVIII.

The figures were drawn with the aid of an Abbé camera lucida, under Zeiss apochromatic obj. 1.5^{mm} N. A. 1.30, combined with compensating ocular 18; except *figs. 13, 14, 133, 134* drawn with compensating ocular 12; *figs. 103, 109, 114–118, 124, 126, 132, 135, 163–171* drawn with ocular 4; and *figs. 65a, 74a, 147a,–153a, 171a′* drawn with compensating ocular 18 under higher magnification obtained when the tube was extended to the furthest point. The plates are reduced one-half the original size, except *plates XXI, XXII* and *XXVIII*, which are reduced two-fifths.

PLATE XIX.

The first mitosis in the germinating tetraspore.

FIG. 1. Nucleus in resting stage, showing delicate linin network and nucleolus.

FIGS. 2a-2c. Three sections of the same nucleus, showing segregation of chromatin material into about 20 groups, probably prochromosomes, before the formation of chromosomes.

FIGS. 3a, 3b. Two sections of the same nucleus, early prophase; 20 chromosomes may be counted.

FIG. 4. The late prophase; centrosome-like bodies lying at each pole.

FIG. 5. Metaphase showing equatorial plate; nuclear membrane still present; neuclear cavity considerably smaller than in the preceding stage.

FIG. 6. Membrane dissolving; centrosphere-like structures present at the poles of the spindle.

FIG. 7. The polar view of an equatorial plate showing 20 chromosomes and the remains of nucleolar material.

FIG. 8. Anaphase, showing groups of daughter chromosomes assembled at the poles of the spindle.

FIG. 9. Late anaphase, the original nuclear membrane entirely dissolved; centrosphere-like structures passing into vaguely outlined kinoplasmic masses.

FIG. 10. Polar view of late anaphase; space within the group of chromosomes probably indicates the first appearance of nuclear sap within a vacuole.

FIG. 11. Telophase; the membrane of the daughter nucleus is clearly formed.

FIG. 12. Resting condition of daughter nucleus, showing linin network and two nucleoli.

FIG. 13. Cleavage furrow appearing at the periphery of the cell in the middle region.

FIG. 14. The cleavage furrow has penetrated almost to the center of the cell, leaving only a narrow passage admitting of protoplasmic continuity between the daughter cells.

PLATE XX.

The first mitosis in the germinating carpospore.

FIG. 15. Nucleus in the resting condition, showing linin network.

FIGS. 16a-16c. Three sections of the same nucleus, showing 40 prochromosomes.

FIGS. 17a, 17b. Two sections of the same nucleus, early prophase; 40 chromosomes are formed.

FIGS. 18a, 18b. Two sections of the same nucleus; centrosome-like bodies occupying pole.

FIG. 19. Metaphase showing equatorial plate; centrosphere-like structures at the poles of spindle.

FIG. 20. Polar view of an equatorial plate showing group of 40 chromosomes and the remains of nucleolar material.

FIG. 21. Anaphase; groups of daughter chromosomes become assembled at the poles of the spindle.

FIG. 22. Later anaphase; original nuclear membrane entirely dissolved; centrosphere-like structures passing into vaguely outlined protoplasmic masses.

FIGS. 23a, 23b. Two sections of the same daughter nucleus in late anaphase viewed from the pole, showing early stage in development of the vacuoles containing nuclear sap.

FIGS. 24–24c. Three sections of the same daughter nucleus shortly after telophase; nuclear membrane clearly formed and two nucleoli present.

FIG. 25. Resting condition of daughter nucleus, showing linin network and nucleolus.

PLATE XXI.

Mitosis in the vegetative cells of the male plant.

FIG. 26. Apical cell of main filament; resting nucleus of an apical cell, showing linin network.

FIG. 27. The same; network becoming coarser.

Figs. 28–35. Apical cells of developing hairs.

FIG. 28. Chromatin granules aggregated into 20 prochromosomes.

FIG. 29. Prophase; 20 chromosomes clearly present; a centrosome-like body at each pole.

FIG. 30. Metaphase showing equatorial plate; centrosphere-like structures at the poles of spindle.

FIG. 31. The polar view of equatorial plate showing 20 chromosomes.

FIG. 32. Late metaphase; two groups of daughter chromosomes just separating.

FIG. 33. Anaphase; two groups of daughter chromosomes separated by a large vacuole which enters between them.

FIG. 34. Telophase; nuclear membrane around the daughter nuclei.

FIG. 35. Later stage than the previous figure; cleavage furrow proceeding inward so as to divide the apical cell.

Mitosis in the vegetative cells of female plants.

Figs. 36–42. Apical cells of developing hairs.

FIG. 36. Prophase of nucleus; centrosome-like body present at the pole.

FIG. 37. Metaphase, showing equatorial plate; centrosphere-like structure conspicuous.

FIG. 38. The polar view of metaphase.

FIG. 39. Late metaphase.

FIG. 40. Anaphase.

FIG. 41. Anaphase; the vacuole beginning to intrude between the groups of daughter chromosomes.

FIG. 42. Telophase; cleavage furrow appearing between the two daughter nuclei.

FIG. 43. Mitotic figure in the old region of thallus, showing large centrosphere-like structures.

FIG. 44. Polar view of the same stage as the above, showing 20 chromosomes.

Mitosis in the vegetative cells of the tetrasporic plant.

Figs. 45–51. All apical cells of main filament.

FIG. 45. Resting nucleus, showing linin network.

FIG. 46. Chromatin granules commence to aggregate to form prochromosomes.

FIG. 47. Early prophase showing 40 chromosomes.

FIG. 48. Metaphase showing equatorial plate; centrosphere-like structures present.

FIG. 49. Late metaphase; groups of daughter chromosomes separated.

FIG. 50. Polar view of metaphase showing 40 chromosomes.

FIG. 51. Anaphase; vacuole intruding between two groups of daughter chromosomes.

PLATE XXII.

Spermatogenesis.

Figs. 52–61. Formation of the sperm mother cell.

FIG 52. Terminal portion of a very young antheridium, consisting of an axial siphon of three cells; the nucleus of the lower cell is in a resting condition; the middle one in early prophase; and the upper one in anaphase.

FIG. 53. Mitotic figure in a cell of the axial siphon to form a stalk cell laterally.

FIG. 54. A cell of the axial siphon with the stalk cell formed laterally.

FIG. 55. Prophase in the stalk cell showing 20 chromosomes.

FIG. 56. Metaphase showing equatorial plate; centrosphere-like structures present.

FIG. 57. Polar view of the same stage as in the preceding figure, showing 20 chromosomes.

FIG. 58. Late metaphase stage; nuclear membrane still present.

FIG. 59. Anaphase; vacuole intruding between two groups of daughter chromosomes.

Fig. 60. Still later stage of anaphase.

FIG. 61. Telophase; cleavage furrow separating the sperm mother cell from the stalk cell.

Figs. 62–74. Formation of the first sperm.

FIG. 62. Resting nucleus of sperm mother cell, showing linin network.

FIG. 63. Fine reticulum transformed into 20 prochromosomes.

FIG. 63a. Portion of *fig. 63* under higher magnification.

FIG. 64. Prophase; a few spindle fibers attached to the chromosomes; centrosome-like bodies at the poles.

FIG. 64a. Portion of *fig. 64* under higher magnification.

FIG. 65. Metaphase; the centrosphere-like structures evident.

FIG. 65a. The nucleus of *fig. 65* under higher magnification.

FIG. 66. The polar view of the stage shown in the previous figure; 20 chromosomes clearly present.

FIG. 67. Late metaphase.

FIG. 68. Anaphase; vacuole intruding between the two groups of daughter chromosomes.

FIG. 69. Later stage of anaphase.

FIG. 70. Lower nucleus passing into resting condition.

FIG. 71. Cleavage furrow separates the sperm above from the sperm mother cell which is destined to produce later a second sperm.

FIG. 72. Sperm almost formed; the sperm mother cell beginning to elongate, preliminary to the development of a second sperm

FIG. 73. Side view of mature sperm

FIG. 74. Sperm viewed from above; chromosomes maintaining their individual forms.

FIG. 74a. Portion of *fig. 74* under higher magnification.

Figs. 75–81. Formation of the second sperm.

FIG. 75. Prophase of mitosis to form second sperm; the first sperm still present at the side, so that the sperm mother cell assumes an asymmetrical outline.

FIG. 76. Metaphase showing equatorial plate; centrosphere-like structures present.

FIG 77. Polar view of same stage as in previous figure.

FIG. 78. Late metaphase.

FIG. 79. Anaphase.

FIG. 80. Later anaphase; vacuole between the two groups of daughter chromosomes.

FIG. 81. Cleavage furrow separating the second sperm from the sperm mother-cell.

PLATE XXIII.

The formation of the procarp.

FIG. 82. Mitotic figure in the cell of the central siphon of a procarp, to form the first peripheral cell; centrosphere-like structures present.

FIG. 83. Polar view of the same mitosis, showing 20 chromosomes.

FIG. 84. First peripheral cell is formed.

FIG. 85. Mitosis to form second peripheral cell.

FIG. 86. Polar view of the same mitosis; 20 chromosomes present.

FIG. 87. Anaphase of the same mitosis.

FIG. 88. The fifth peripheral cell, called the pericentral cell, formed on the left of the central siphon; this cell is destined to develop the carpogonial branch.

FIG. 89. Mitosis to form first cell of the carpogonial branch from the pericentral cell.

FIG. 90. Polar view of the same stage as the previous figures, showing 20 chromosomes.

FIG. 91. Anaphase.

FIG. 92. Late anaphase.

FIG. 93. Telophase; vacuole intruding between the daughter nuclei.

FIG. 94. Mitotic figure to form second cell of the carpogonial branch; *pc*, pericentral cell.

FIG. 95. Polar view of the same stage as shown in the previous figure; 20 chromosomes readily seen.

FIG. 96. Mitotic figure forming the third cell of the carpogonial branch.

FIG. 97. Polar view of the same stage.

FIG. 98. Mitotic figure to form the fourth cell of the carpogonial branch.

FIG. 99. Polar view of the previous figure.

FIG. 100. Mitosis of the nucleus within the fourth cell of carpogonial branch, which develop the trichogyne and carpogonium; this mitosis gives two daughter nuclei as shown in *fig. 101*; being cut obliquely, the chromosomes, 20 in number, may be counted.

FIG. 101. The two nuclei within the carpogonium or the fourth cell of the carpogonial branch: *pc*, pericentral cell.

PLATE XXIV.

Development of the trichogyne.

FIG. 102. Development of the trichogyne from the carpogonium.

FIG. 103. A mature procarp in section, showing the situation of the carpogonial branch: *pc*, pericentral cell; *as*, axial siphon.

FIG. 104. Carpogonium with trichogyne at maturity; note the difference in size between the sister nuclei, for the carpogonium with its nucleus has enlarged greatly.

Fertilization.

FIG. 105. Sperm attached at the tip of the trichogyne.

FIG. 106. Contacts of sperm, its nucleus passing into trichogyne; note the individual chromosomes in the sperm nucleus.

FIG. 107. Sperm cell emptied of contents; sperm nucleus about to pass the trichogyne nucleus.

FIG. 108. Sperm nucleus having passed the trichogyne nucleus is about to enter the carpogonium.

FIG. 109. Section of procarp showing the situation of the carpogonium at the time of fertilization.

FIG. 109a. The carpogonium of *fig. 109* under higher magnification; sperm nucleus about to fuse with the female nucleus, which has moved upwards in the carpogonium.

FIG. 110. Mitotic figure in the formation of an auxiliary cell from the pericentral cell, which takes place parallel with the nuclear fusion in the carpogonium.

FIG. 111. Prophase of the above mitosis showing 20 chromosomes.

FIG. 112. Mitosis in a cortical cell of the procarp.

FIG. 113. Polar view of the above mitosis, showing 20 chromosomes.

FIG. 114. Section of procarp showing situation of the carpogonium at the time of contact between the sperm and carpogonium nuclei.

FIG. 114a. The carpogonium of *fig. 114* under higher magnification; the sperm nucleus beginning to fuse with the female; no membrane observable around the sperm nucleus since the beginning of entry of it into the trichogyne; the female nucleus in resting condition.

FIG. 115. Section of procarp showing carpogonium at a late stage in the fusion of the sexual nuclei.

FIG. 115a. The carpogonium of *fig. 115* under higher magnification; the chromosomes of the sperm nucleus beginning to separate in the female nucleus; the network in female nucleus preparing to form chromosomes.

FIG. 116. The fusion nucleus in the carpogonium after the female chromosomes have been formed, showing a mingling of male and female; the total number of chromosomes is 40.

Development of the cystocarp.

FIG. 117. Section of procarp at the time of the first mitosis of the fusion nucleus within the carpogonium.

FIG. 117a. The carpogonium of *fig. 117* under higher magnification, showing the first mitosis of the fusion nucleus.

FIG. 118. Procarp showing the first mitosis of the fusion nucleus in the carpogonium; cut obliquely.

FIG. 118a. The carpogonium of *fig. 118* under higher magnification, showing a polar view of first mitosis of the fusion nucleus; 40 chromosomes present.

FIG. 119. Prophase of a nucleus within the first cell of the carpogonial branch.

FIG. 120. Metaphase of the above mitosis.

FIG. 121. Polar view of the same mitosis showing 20 chromosomes.

FIG. 122. Anaphase of the same mitosis.

PLATE XXV.

FIGS. 123a, 123b. Two sections of the fusion nucleus at metaphase of the first mitosis.

FIG. 124. Section of the procarp at anaphase of the first mitosis of the fusion nucleus within the carpogonium.

FIG. 124a. The carpogonium of *fig. 124* under higher magnification.

FIG. 125. Migration of one of two daughter nuclei (sporophytic), resulting from the first mitosis of the fusion nucleus, into the third auxiliary cell (compare with *a3* in *diagram 3*).

FIG. 126. Migration of two daughter nuclei (sporophytic) into the pericentral cell, the third auxiliary cell having fused with it; a nucleus from one of the auxiliary cells below also entering the pericentral cell; the first, second, and third cells of the carpogonial branch, together with the carpogonium, about to collapse.

FIG. 127. Mitoses of two sporophytic nuclei derived from the fusion nucleus and of a gametophytic nucleus also within the central cell; the distinction between

the mitotic figures is readily seen by estimating the number of chromosomes arranged in the equatorial plate.

FIG. 128. Sporophytic nucleus in a process from the central cell, from which after a mitosis a carpospore will be formed; the nucleus in prophase; 40 chromosomes may be counted.

FIG. 129. Metaphase of the mitosis which separates the carpospore from the stalk cell.

FIG. 130. Polar view of the same mitosis cut obliquely, showing 40 chromosomes.

FIG. 131. Telophase of the same mitosis; the upper nucleus will lie in the carpospore.

FIG. 132. Section of a cystocarp, showing central cell (*cc*), stalk cell (*sc*), carpospore (*sp*), and paranematal filaments (*pf*).

FIG. 133. Stalk cells beginning to fuse together side by side, and their nuclei, with other nuclei remaining in the central cell, beginning to disorganize.

FIG. 134. Disorganizing nuclei in the central cell.

FIGS. 135a–135d. Four sections of a procarp, showing the arrangement of the auxiliary cells (compare with *diagram 3*); the fusion nucleus in the carpogonium (*carp*) shows the mingling of male and female chromosomes.

PLATE XXVI.

The tetraspore formation.

FIG. 136. Prophase in a cell of the central siphon previous to the formation of pericentral cell, showing 40 chromosomes.

FIG. 137. Metaphase of this mitosis.

FIG. 138. Anaphase.

FIG. 139. Polar view of anaphase; 40 chromosomes present.

FIG. 140. Tip of a filament, showing stages in the formation of the tetraspore mother-cell; *pc*, pericentral cell; *sc*, stalk cell; *tmc*, tetraspore mother cell.

FIG. 141. Chromatin network in resting nucleus of pericentral cell.

FIG. 142. Metaphase of the mitosis in the pericentral cell; centrosphere-like structures present.

FIG. 143. Late metaphase of the same.

FIG. 144. Anaphase.

FIG. 145. Telophase; vacuole intruding between the daughter nuclei.

FIG. 146. Tetraspore mother cell becoming separated from the stalk cell by the cleavage furrow.

FIG. 147. Later stage of the above; tetraspore mother cell increased in size; the nucleus with delicate linin network.

FIG. 147a. Portion of linin reticulum in *fig. 147* under higher magnification.

FIG. 148. Reticulum becoming transformed into a coarser chromatin network with here and there large knots upon the threads.

FIG. 148a. Portion of network from *fig. 148* under higher magnification.

FIG. 149. Irregular network becoming transformed into more even threads.

FIG. 149a. Portion of threads from *fig. 149* under higher magnification.

FIG. 150. Threads becoming arranged parallel to one another.

FIG. 150a. Portion of threads from *fig. 150* under higher magnification.

FIG. 151. Synapsis.

FIG. 151a. Portion of the parallel threads from *fig. 151* fusing in parts, under higher magnification.

FIG. 152. Nucleus emerging from synapsis.

FIG. 152a. Portion of fused parallel threads or spirem from *fig. 152* under higher magnification; the spirem beginning to split longitudinally.

FIG. 153. Later stage than the above; spirem beginning to segment to form chromosomes; the split segments arranged side by side.

FIG. 153a. Segments of spirem from *fig. 153* under higher magnification, showing X and double L and V forms.

PLATE XXVII.

FIG. 154. Early prophase of mitosis in tetraspore mother cell; 20 bivalent chromosomes are present.

FIG. 154a. Chromosomes from *fig. 154* under higher magnification, showing bivalent character.

FIG. 155. Later prophase; bivalent chromosomes have been shortened.

FIG. 156. Metaphase; a great number of chromosomes (about 80) arranged in the equatorial plate; this large number results from the premature division of the halves of the bivalent chromosomes shown in *fig. 155;* the 80 chromosomes are therefore granddaughter chromosomes, which will be distributed to the four tetraspores; centrosphere-like structures poorly differentiated.

FIG. 157. Later metaphase of the first mitosis; two groups of daughter chromosomes, 40 in each, just separating and the four poles of second spindle already differentiated.

FIG. 158. Metaphase of second mitosis; four groups of granddaughter chromosomes (three seen) passing to the poles.

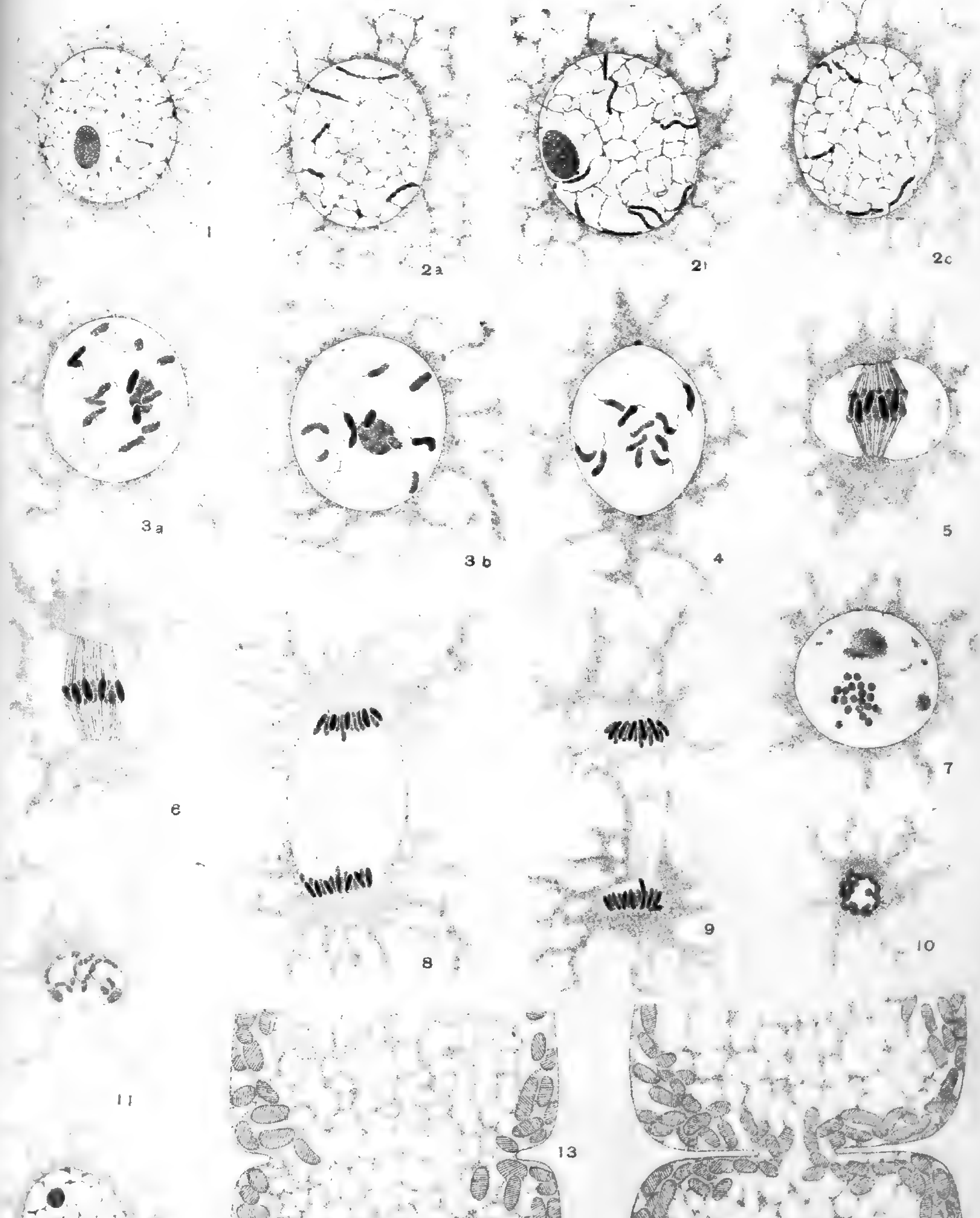
FIG. 159. Groups of granddaughter chromosomes at the poles; nucleolus has appeared in the center of the nuclear space.

FIG. 160. Groups of granddaughter chromosomes forming chromatin network; membrane surrounding the nuclear cavity assuming a tetrahedral shape with kinoplasm accumulating at the corners.

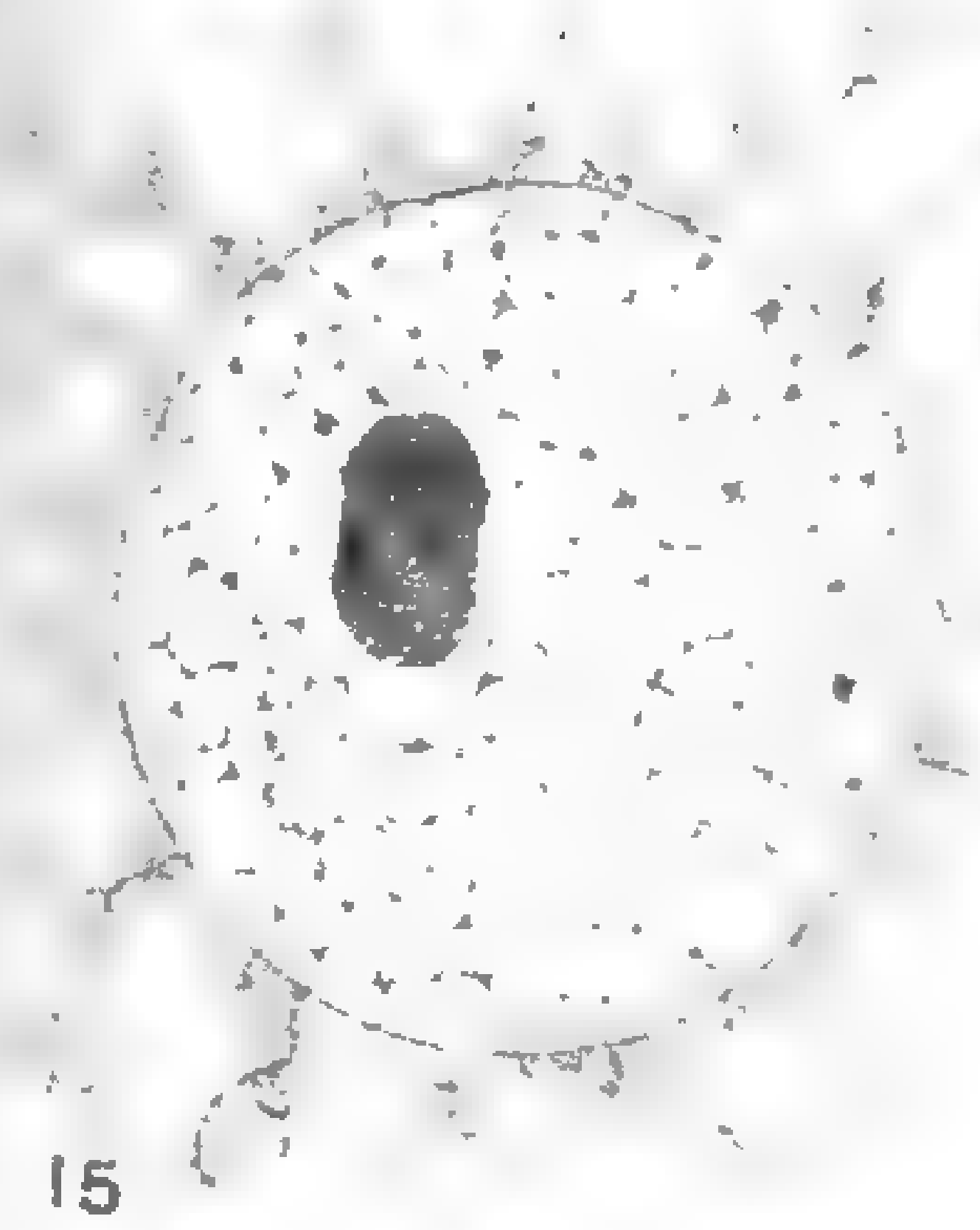
FIG. 161. Groups of granddaughter chromosomes have formed an anastomosing chromatin network; membrane surrounding nuclear cavity has broken in the region between the four poles so as to admit the entrance of kinoplasmic fibrils without the membrane; the fibrils grow toward the center of the nuclear cavity.

FIG. 162. Daughter nuclei becoming separated by the growth of kinoplasm which surrounds the chromatin network.

FIG. 163. Tetraspore mother cell at the time of separation of the daughter nuclei.



YAMANOUCHI on POLYSIPHONIA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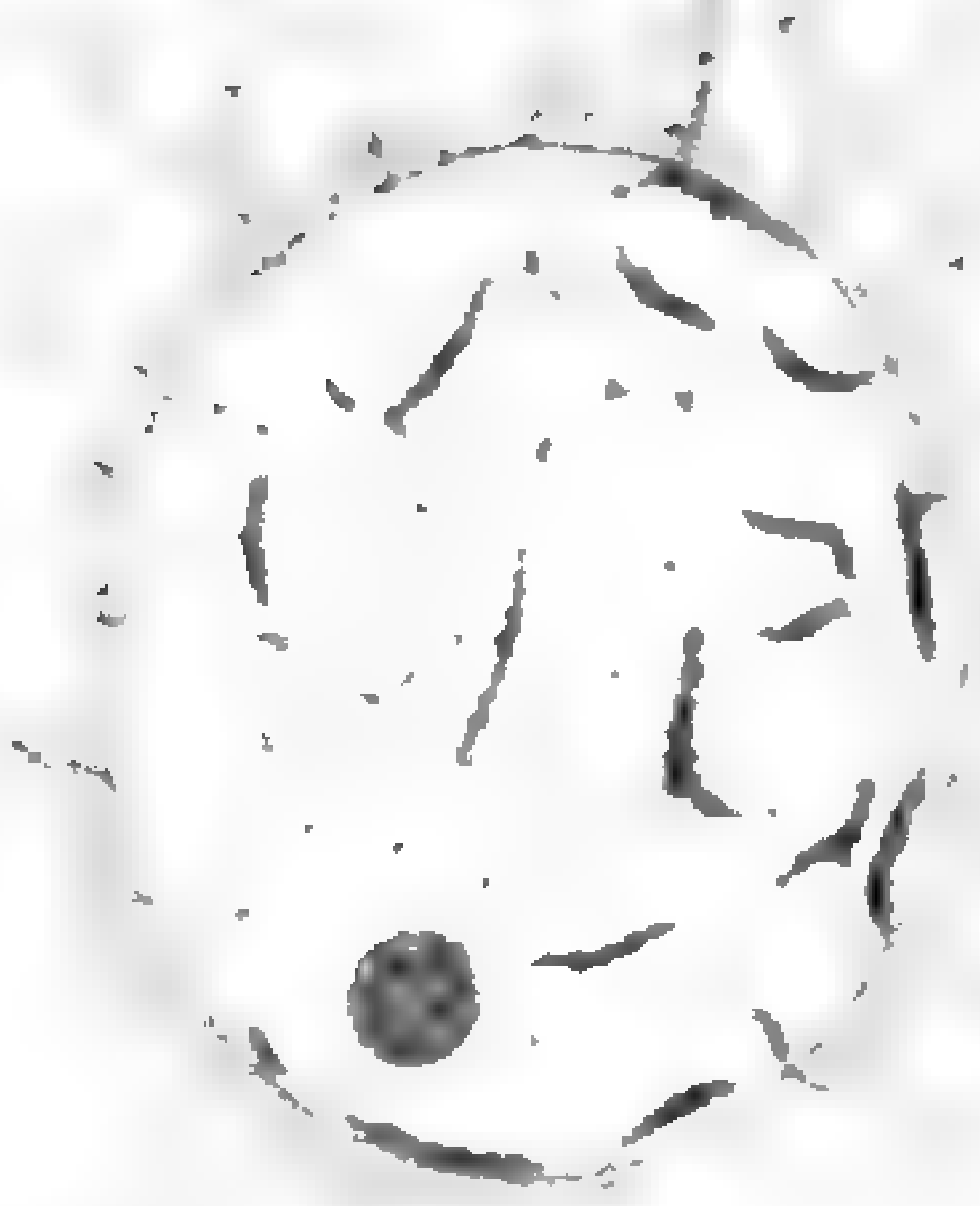
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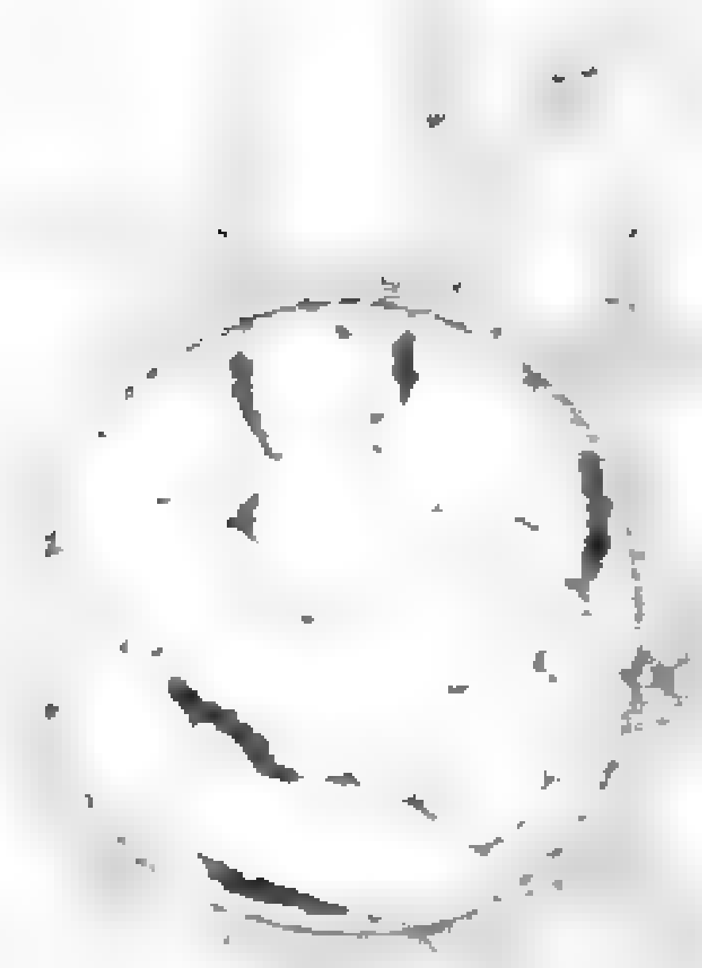
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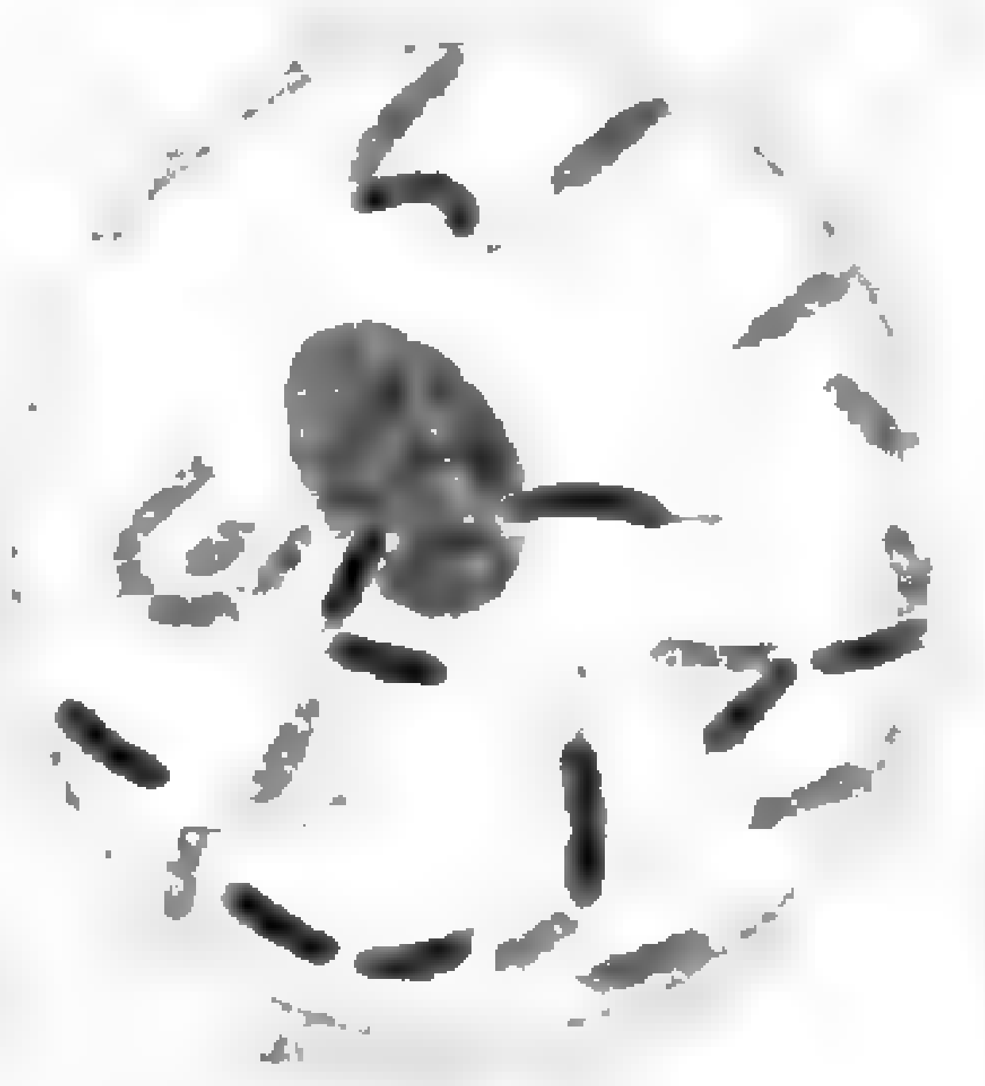
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18a


18b


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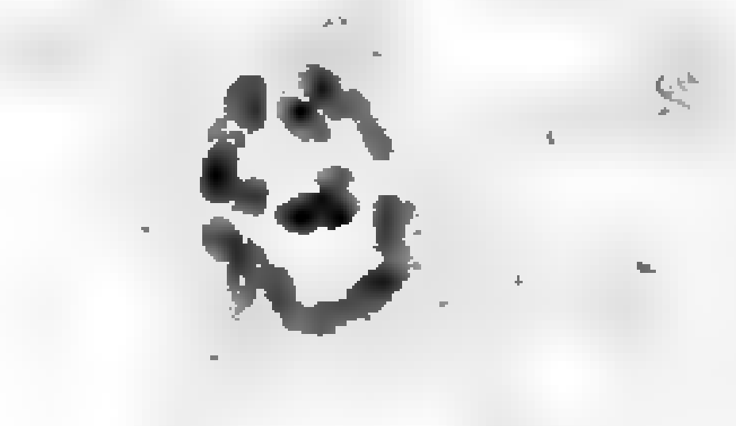
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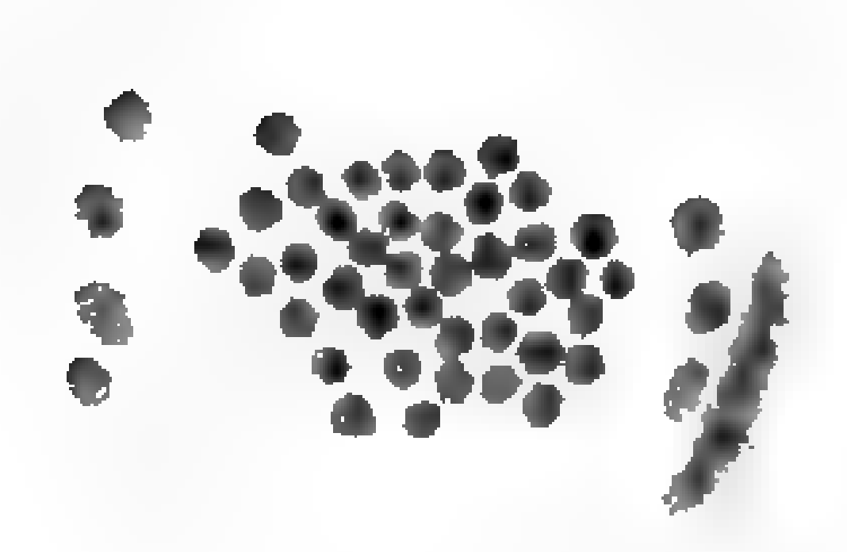
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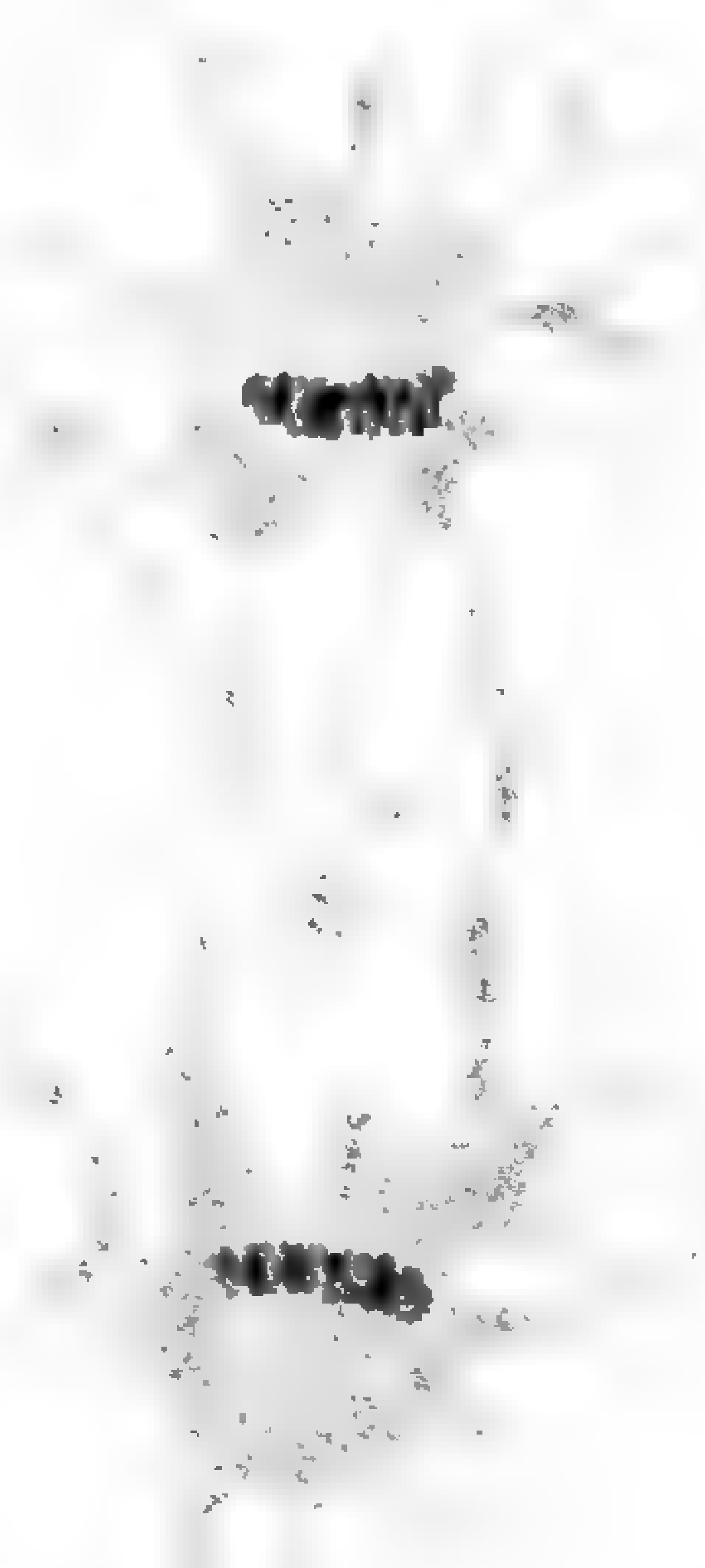
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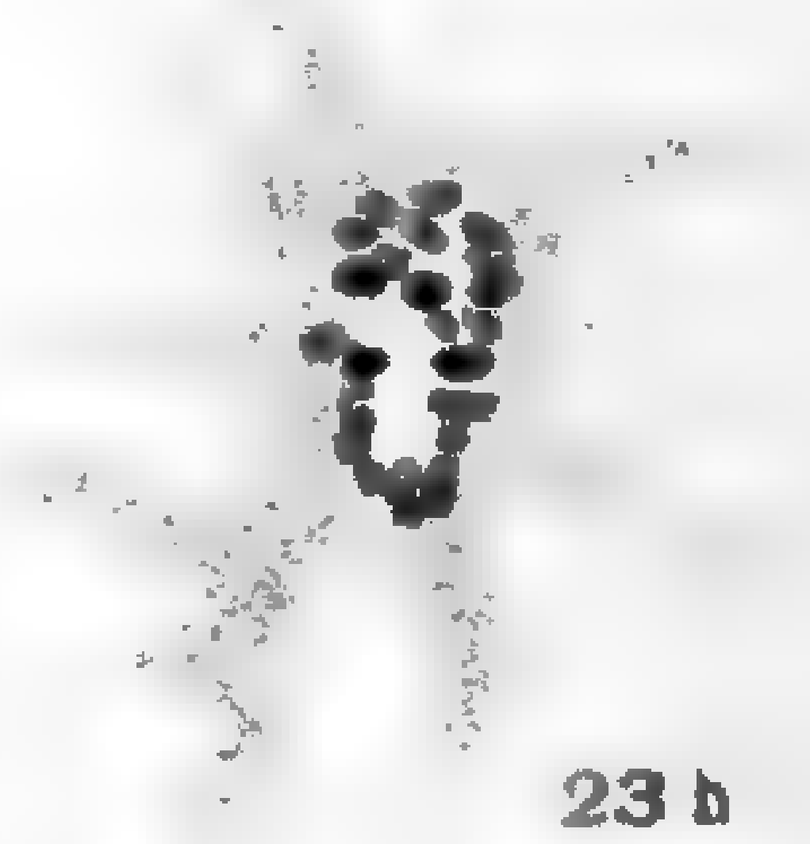
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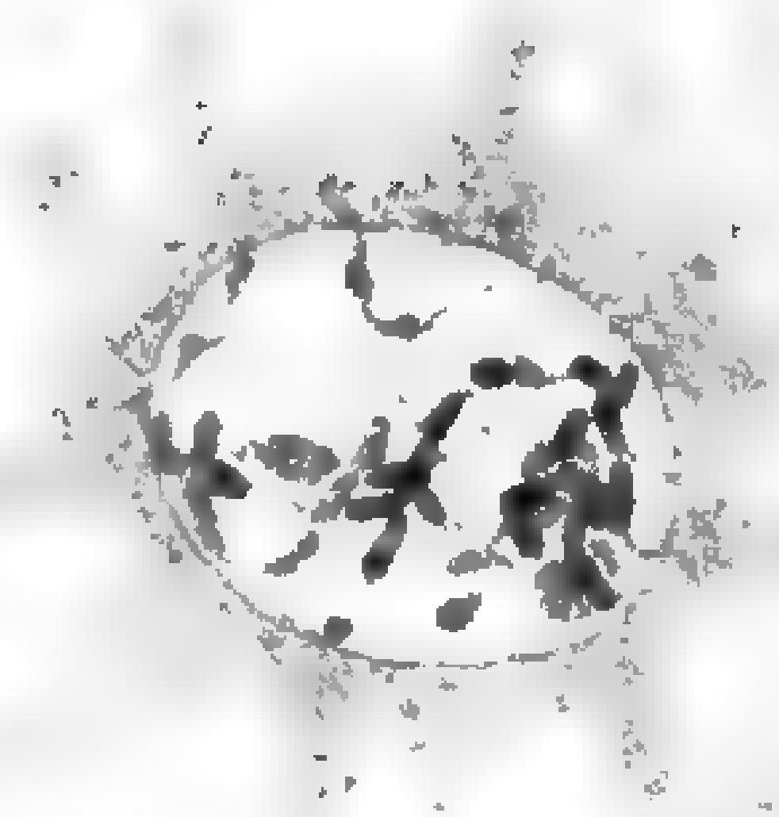
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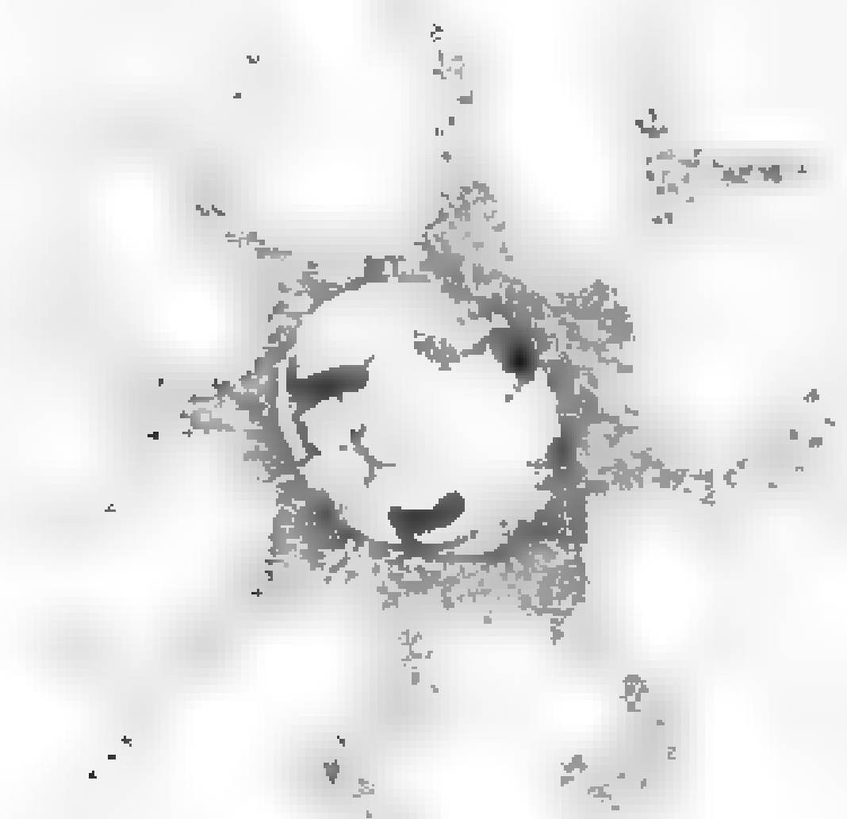
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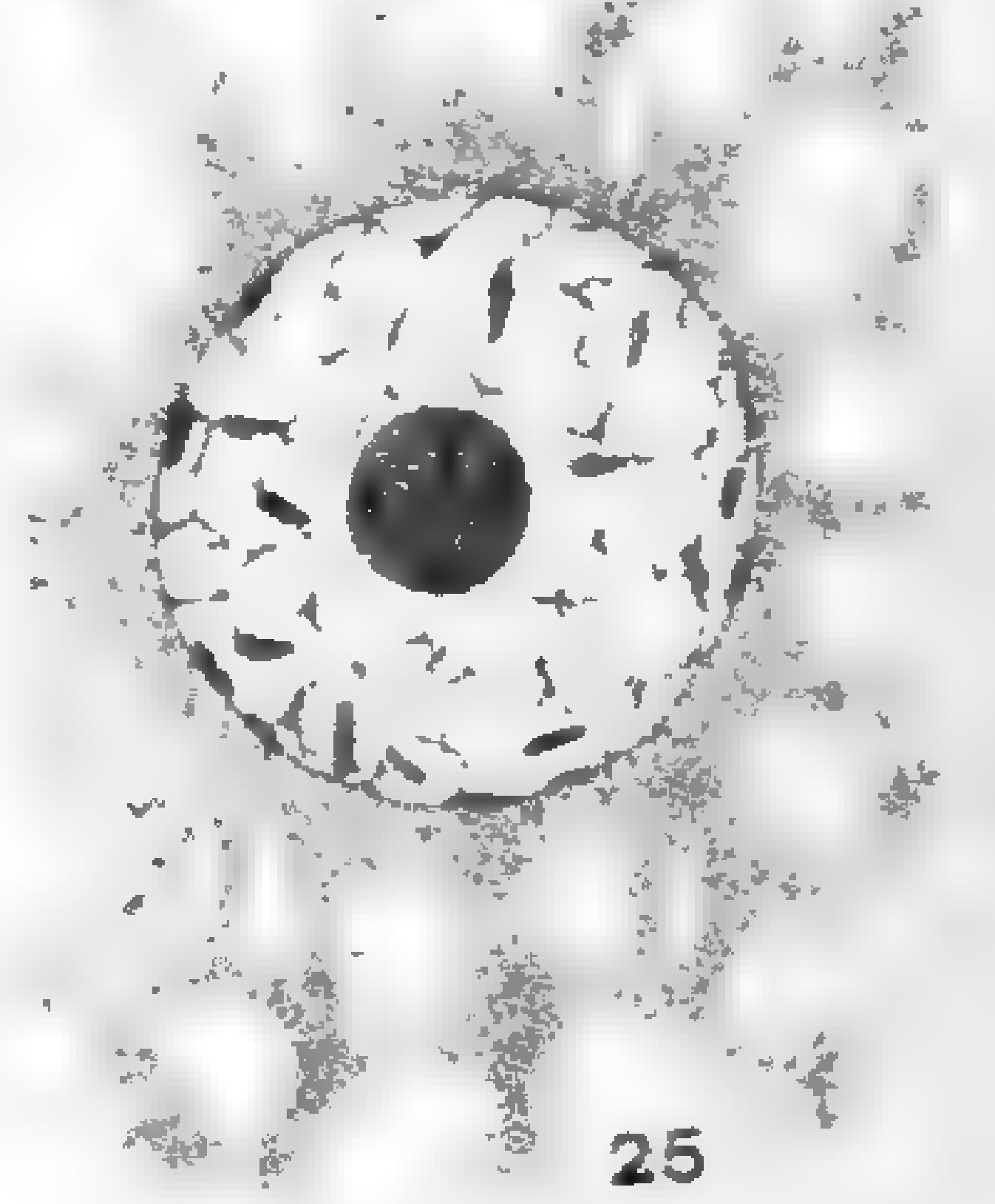
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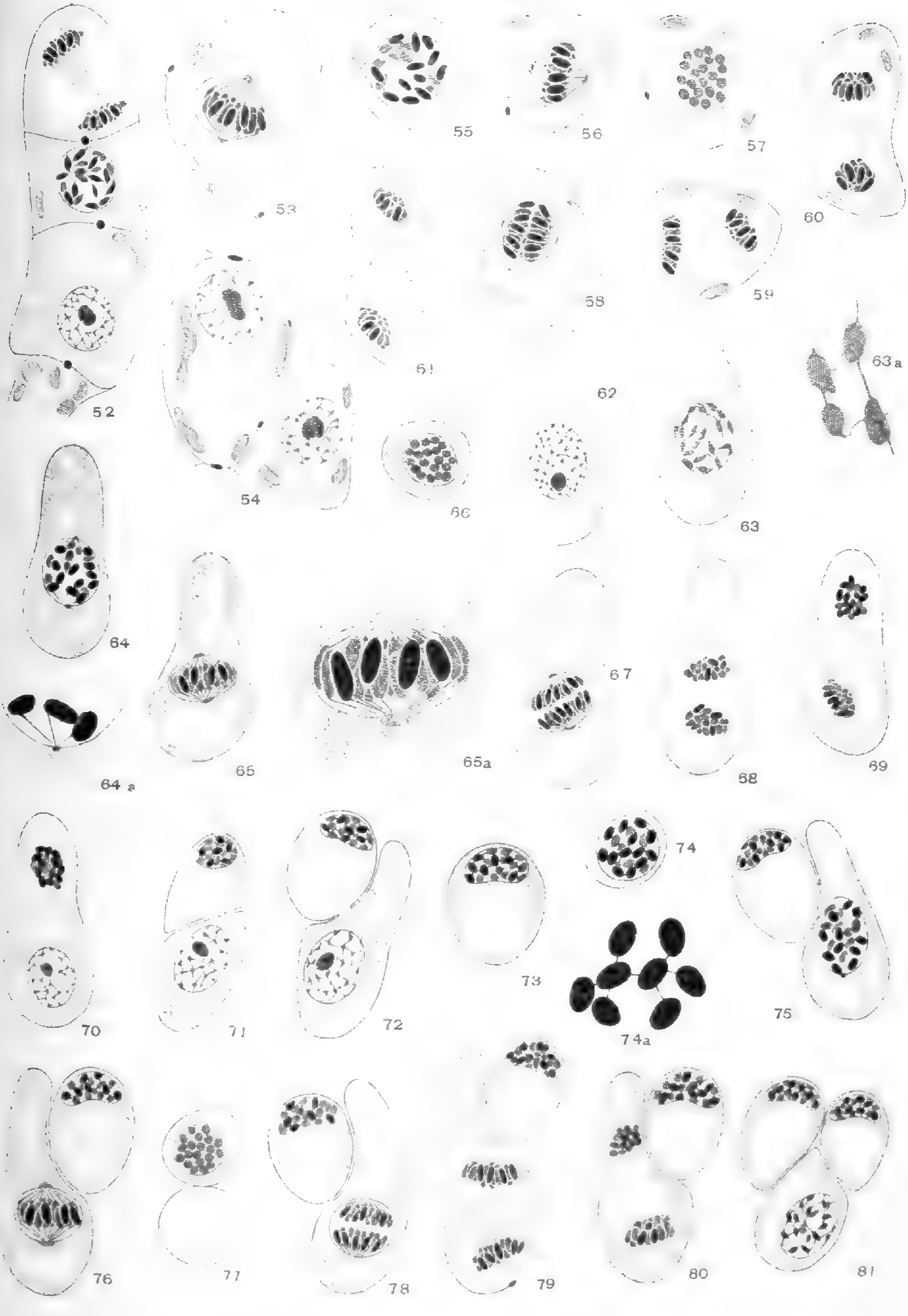

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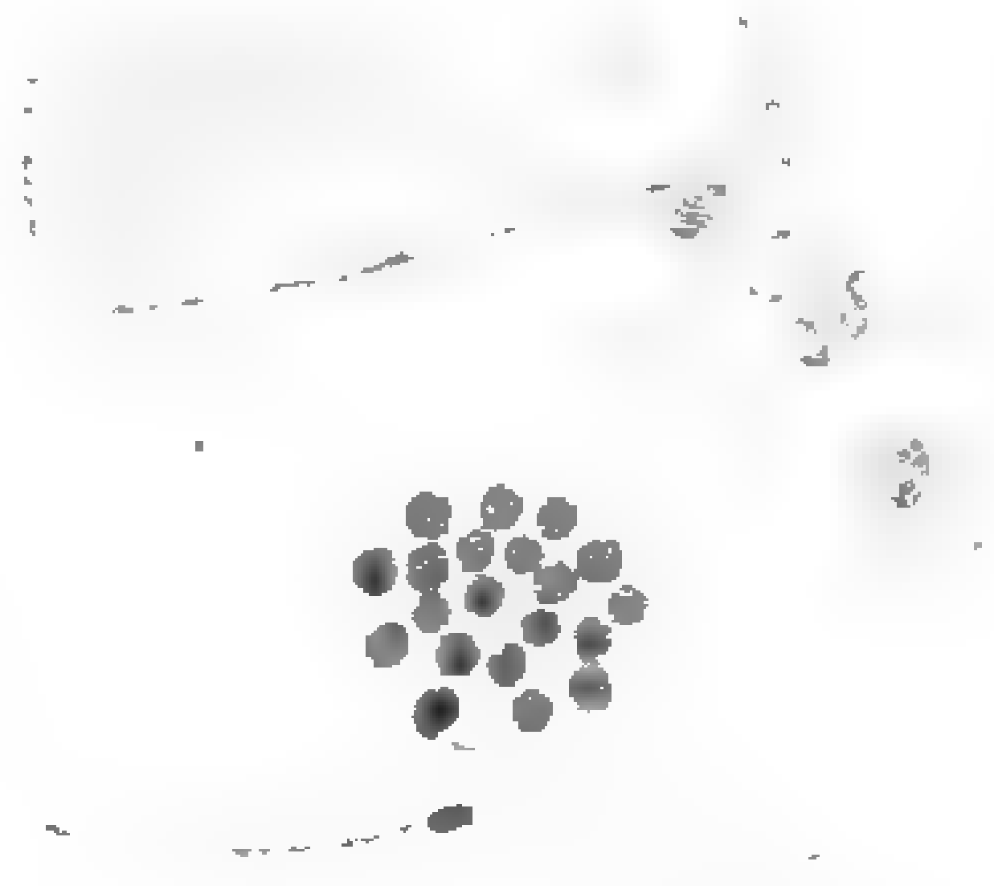
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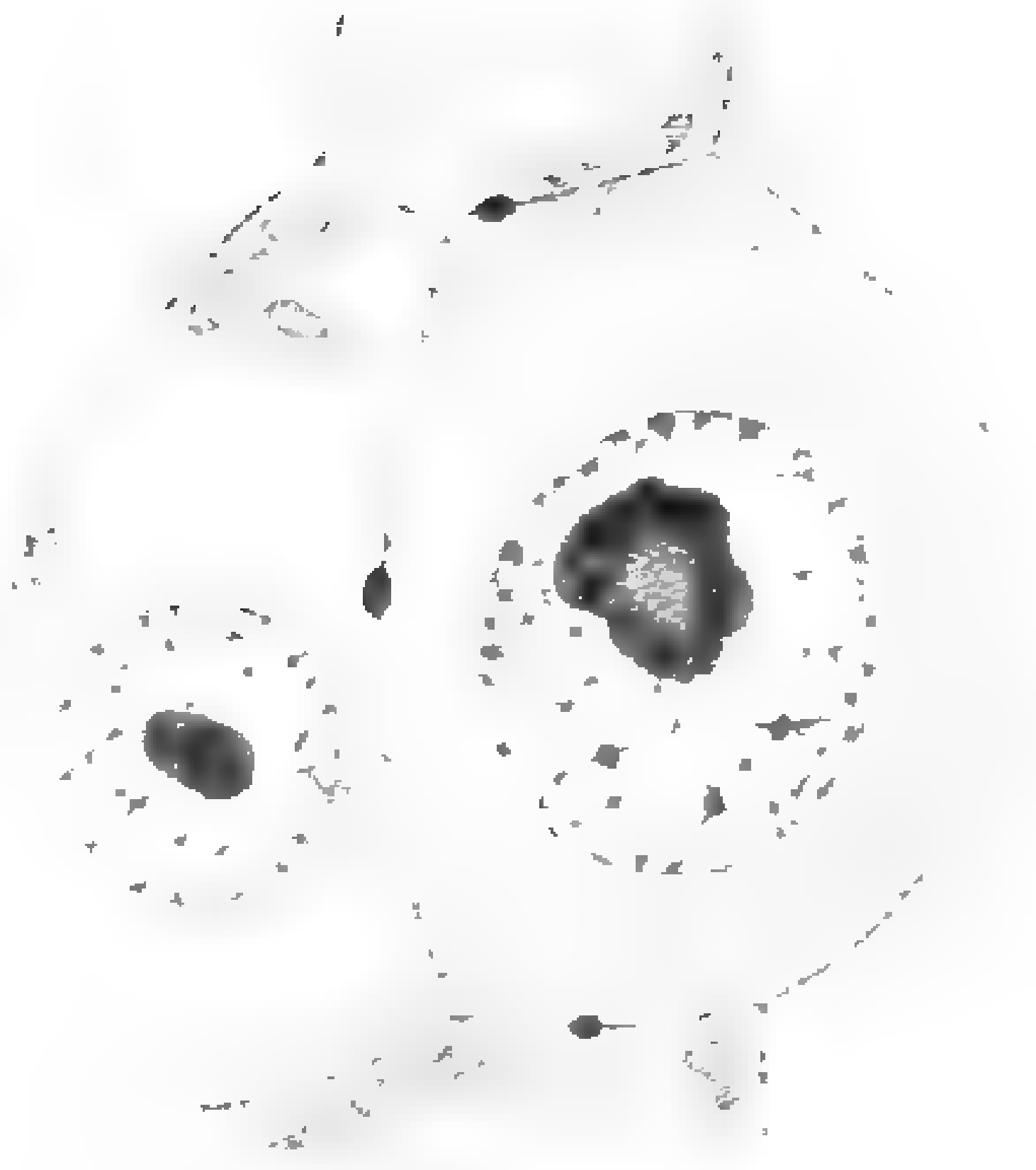
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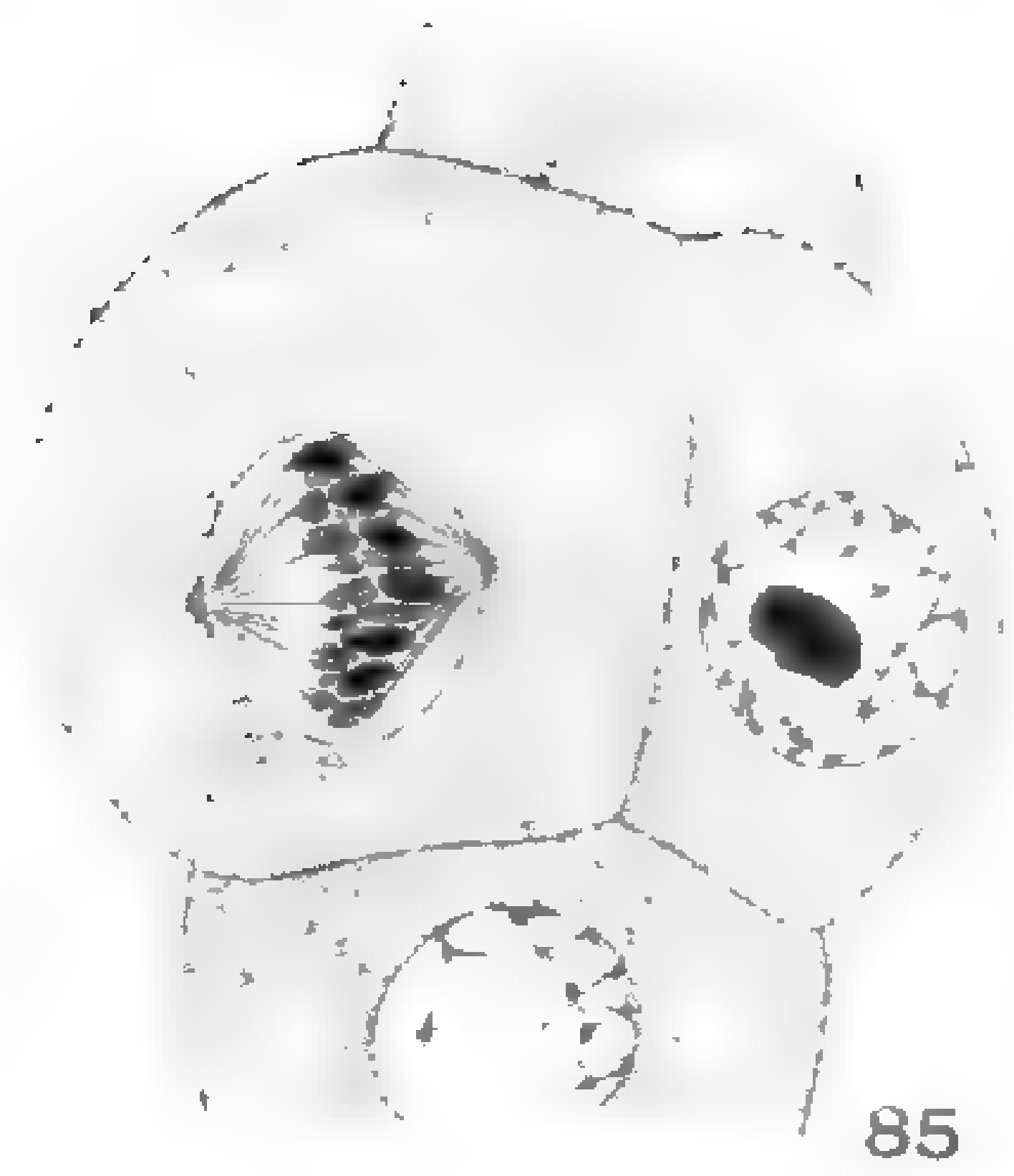
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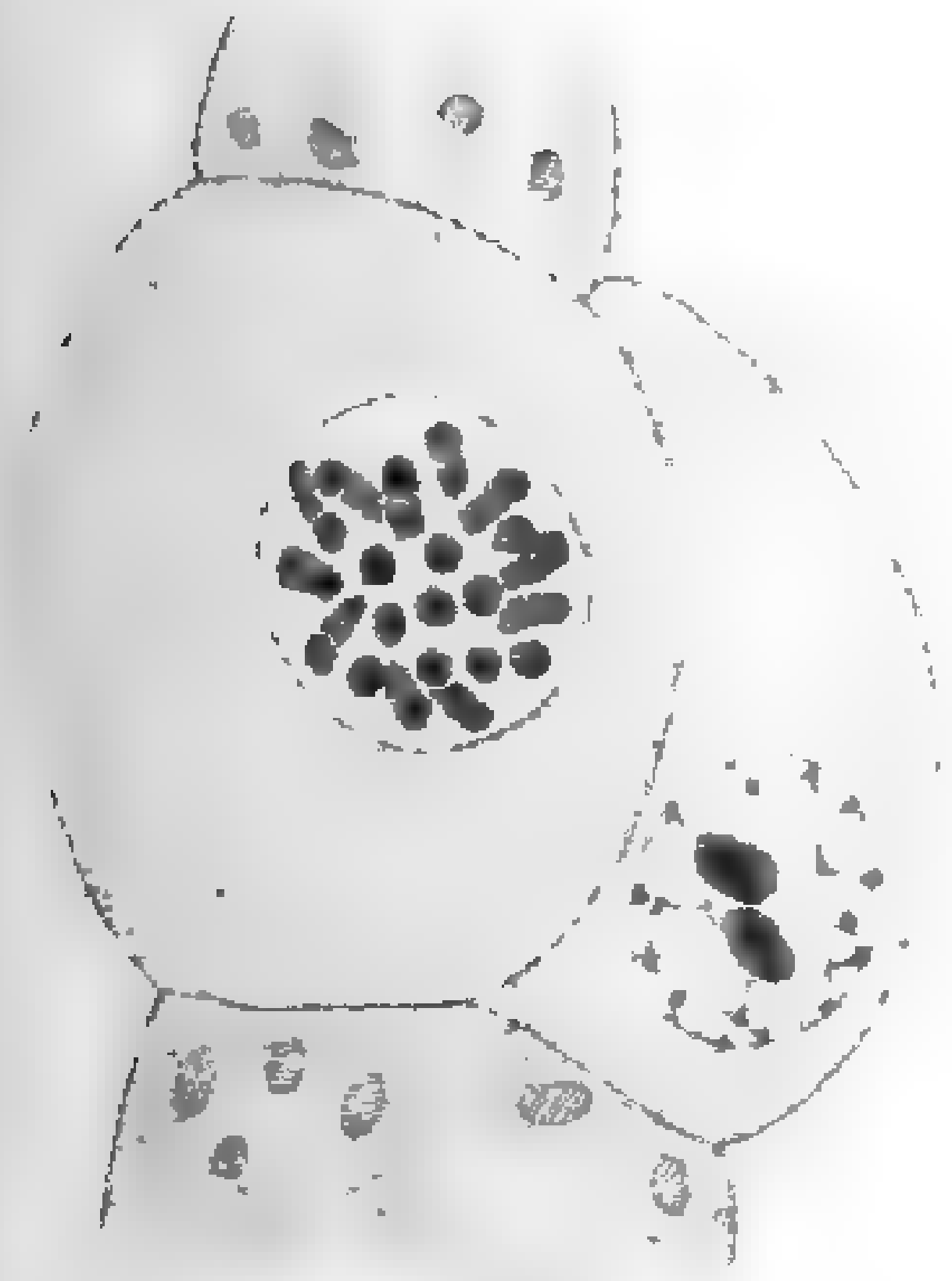
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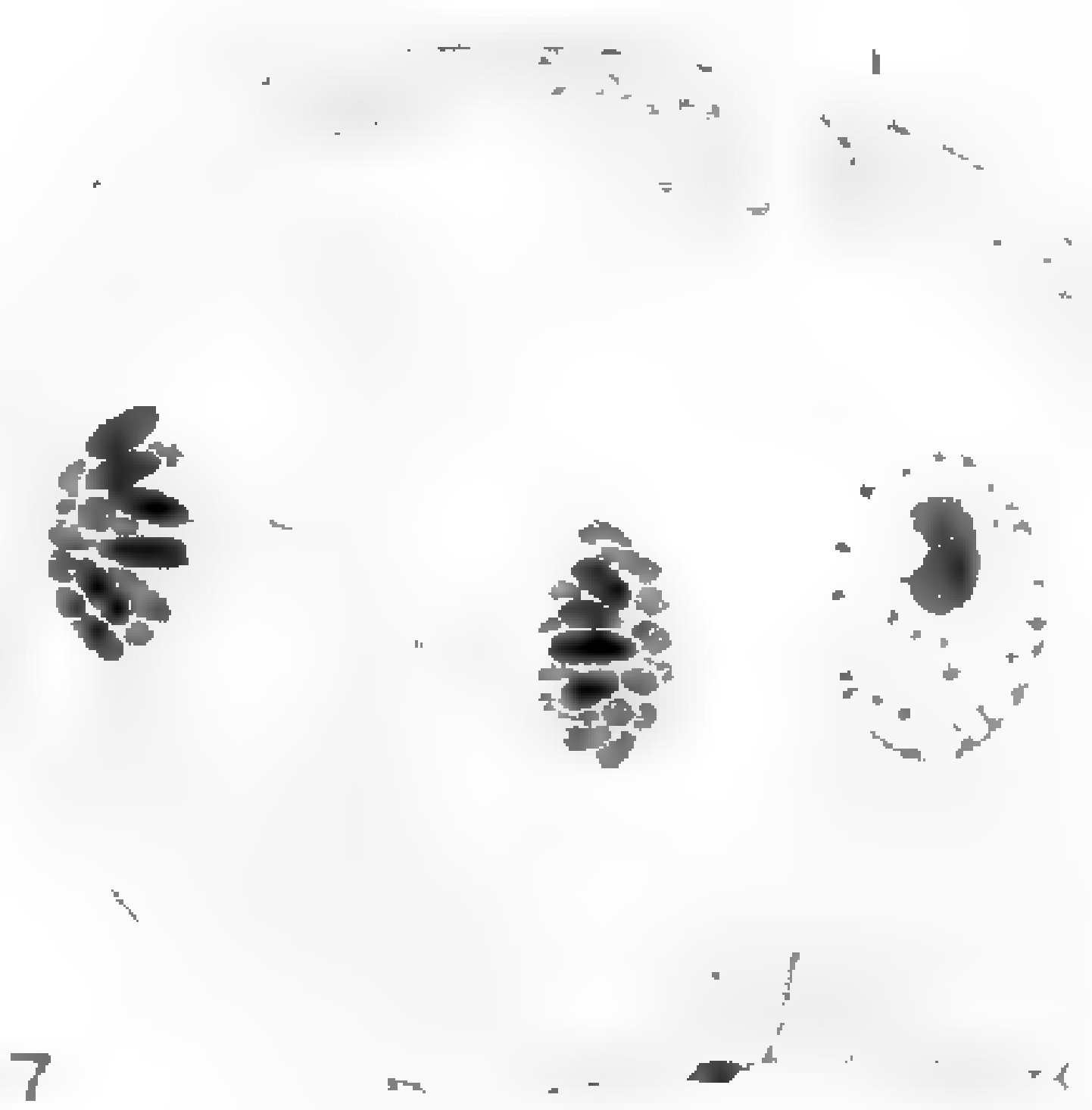
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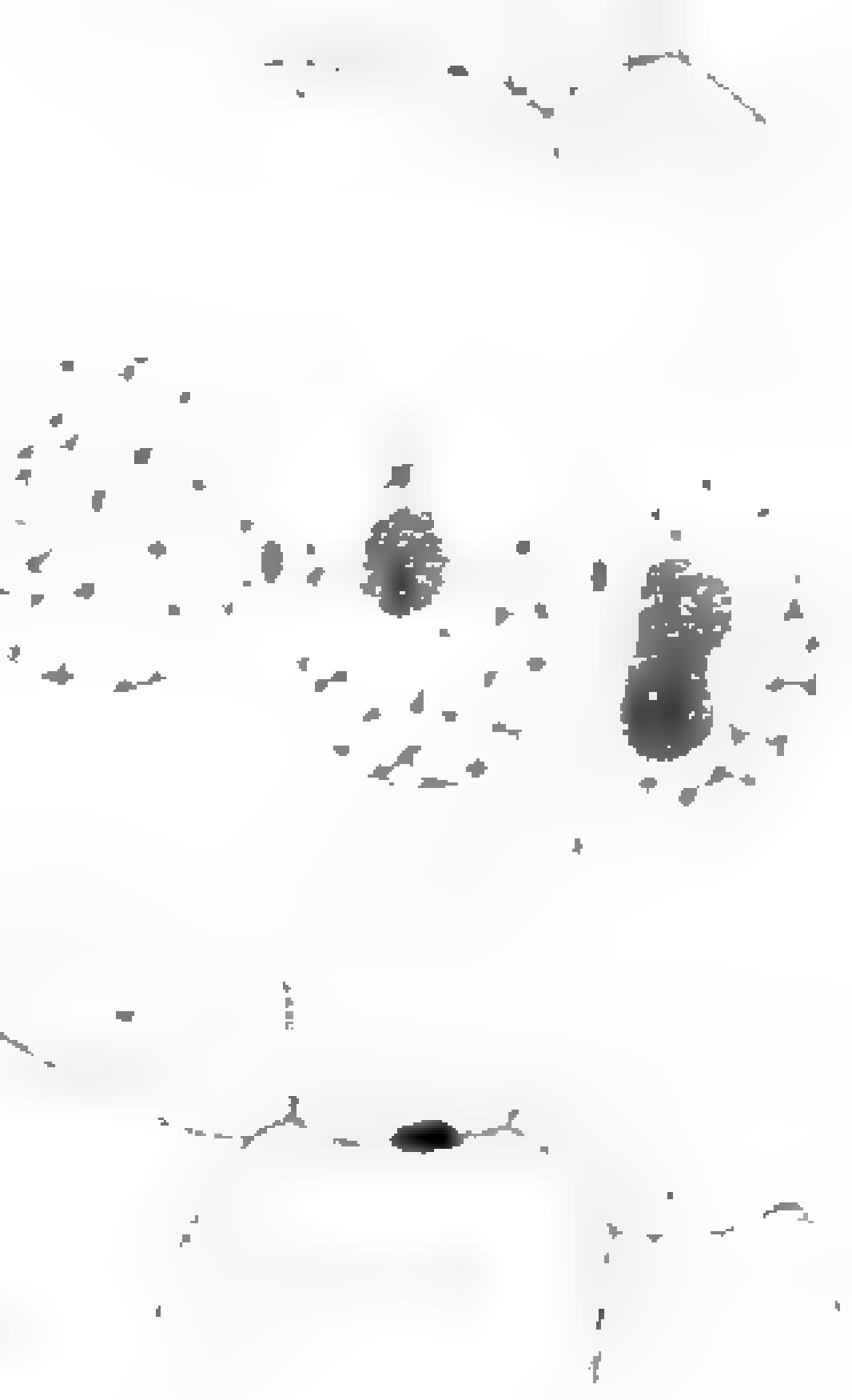
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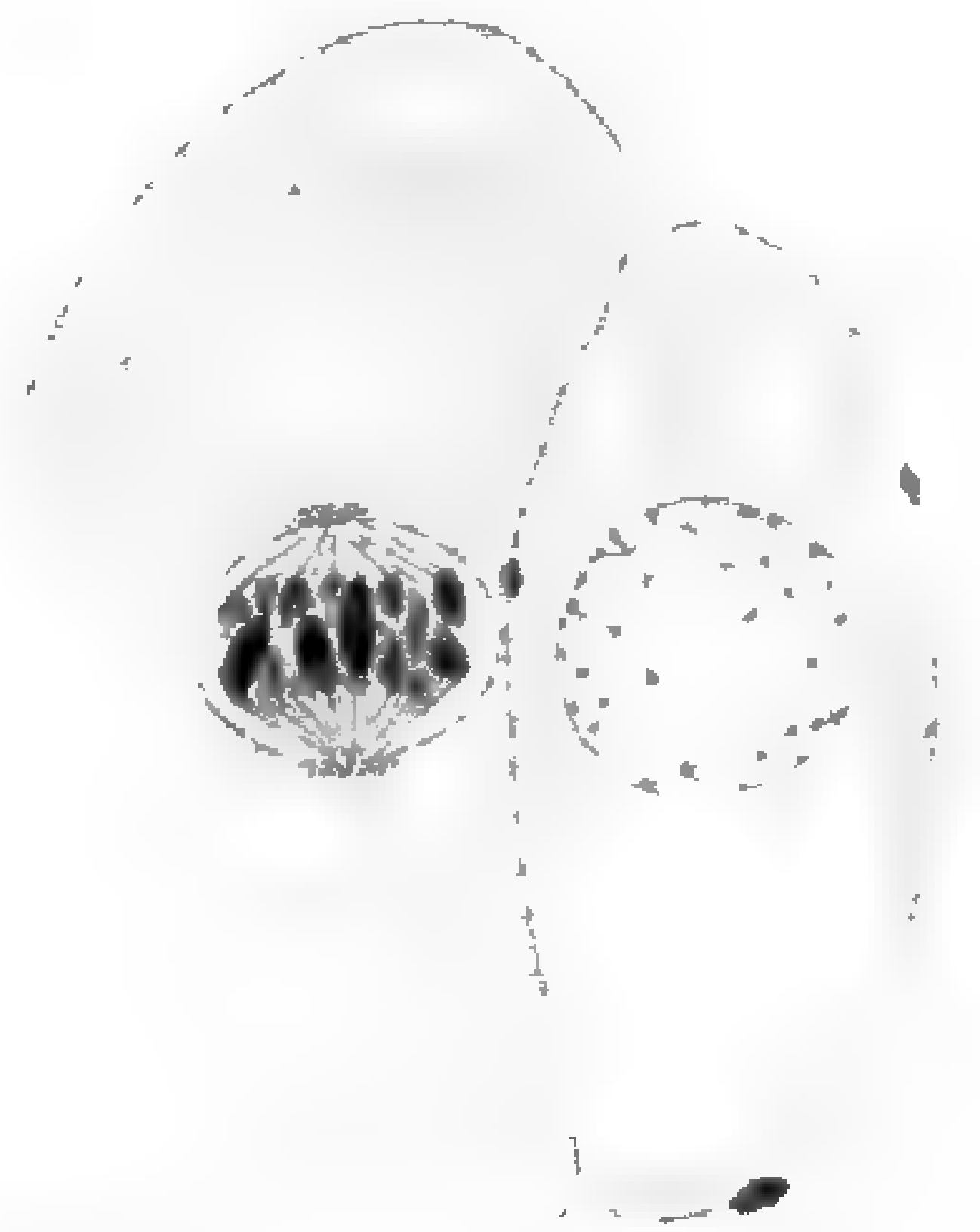
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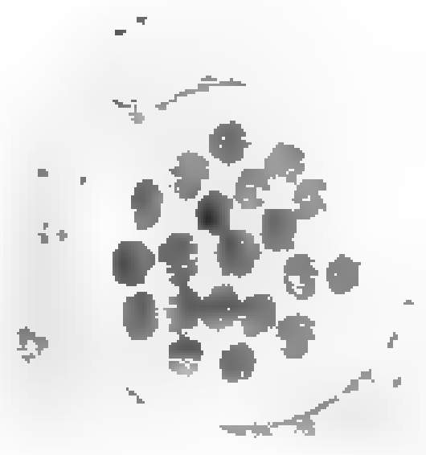
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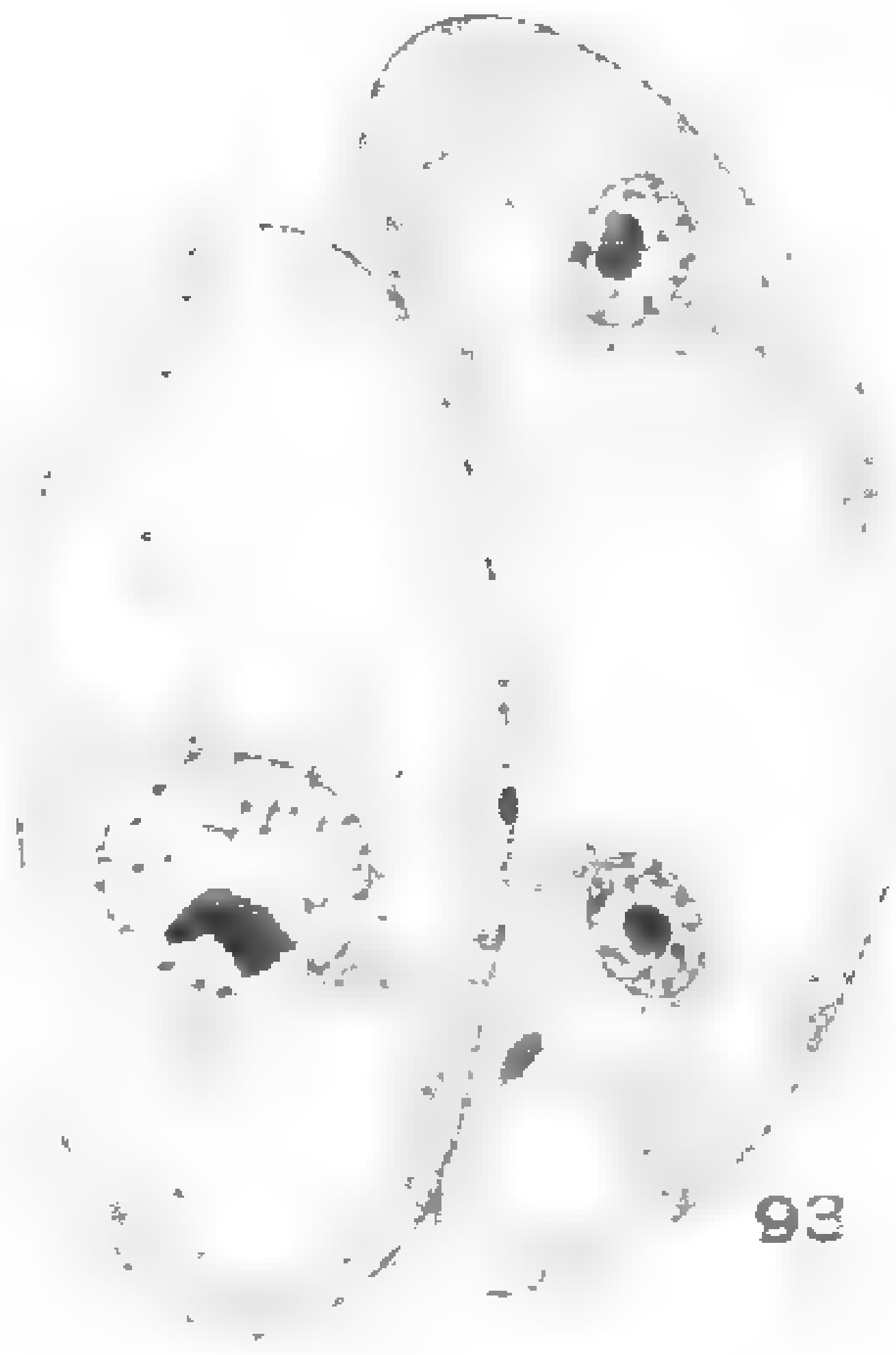
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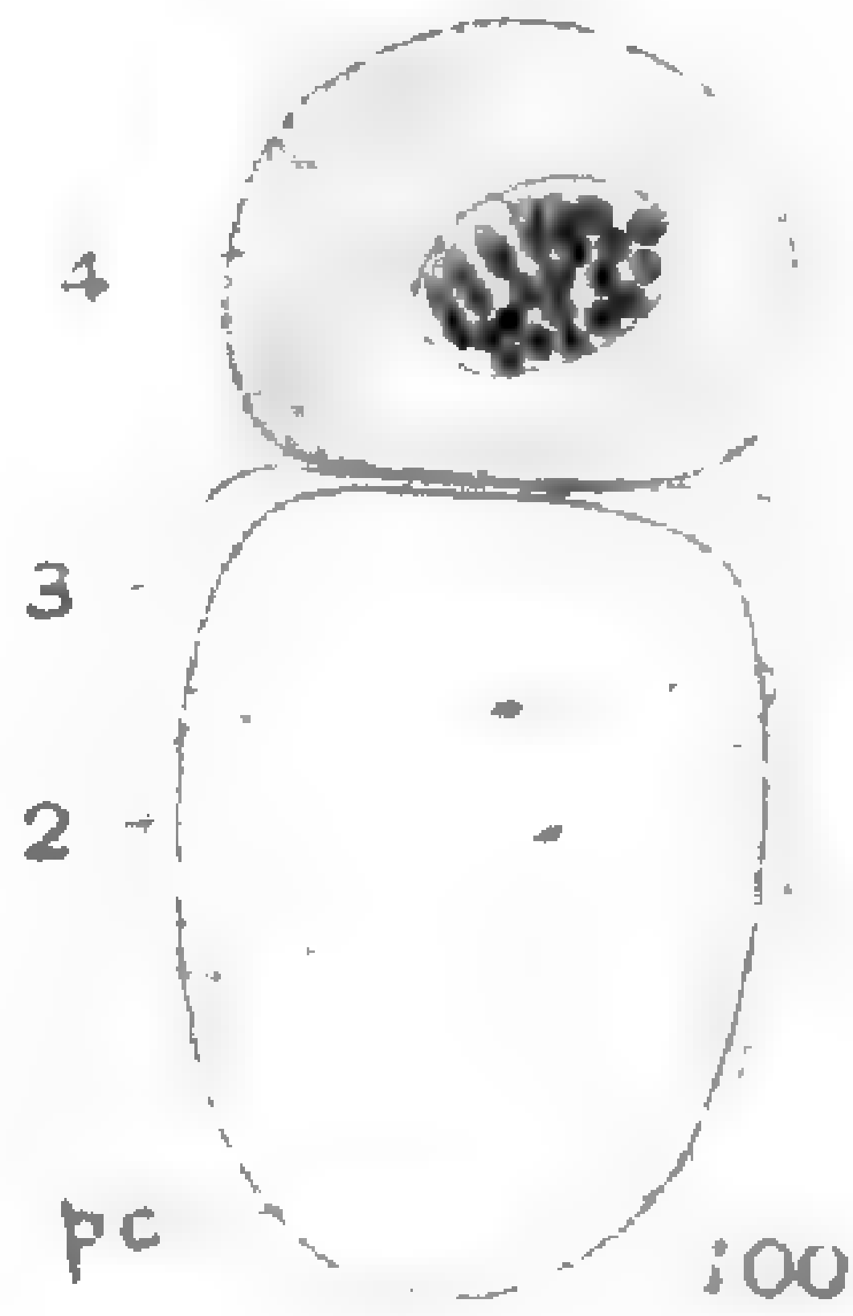

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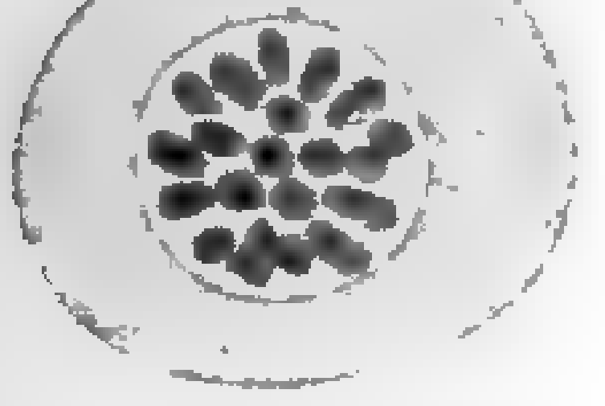
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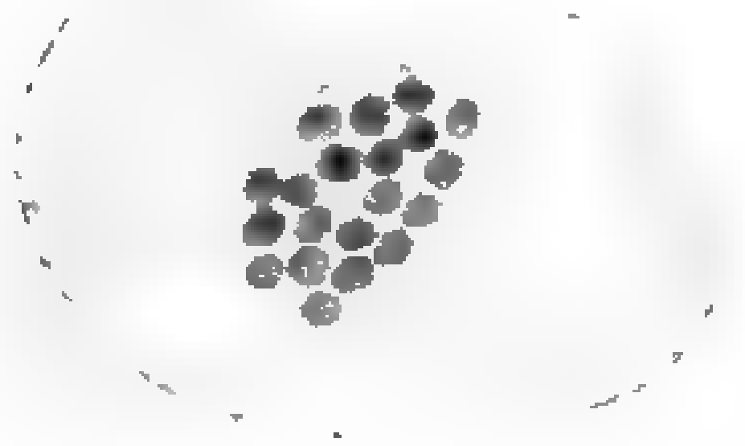
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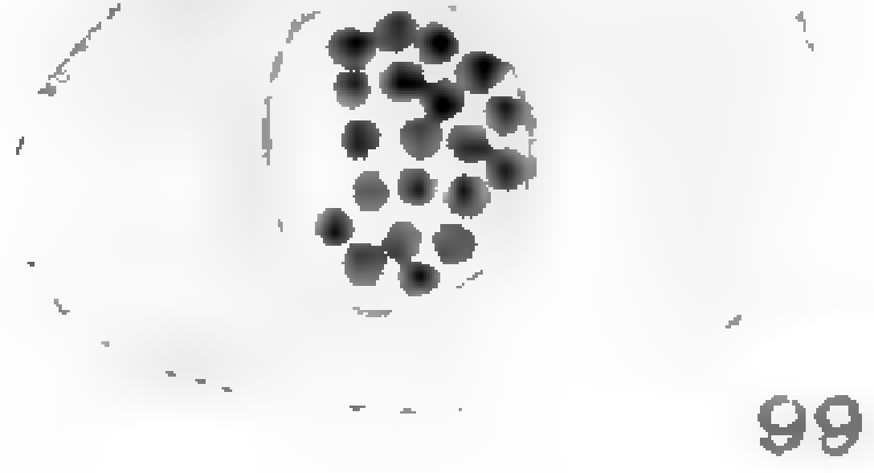
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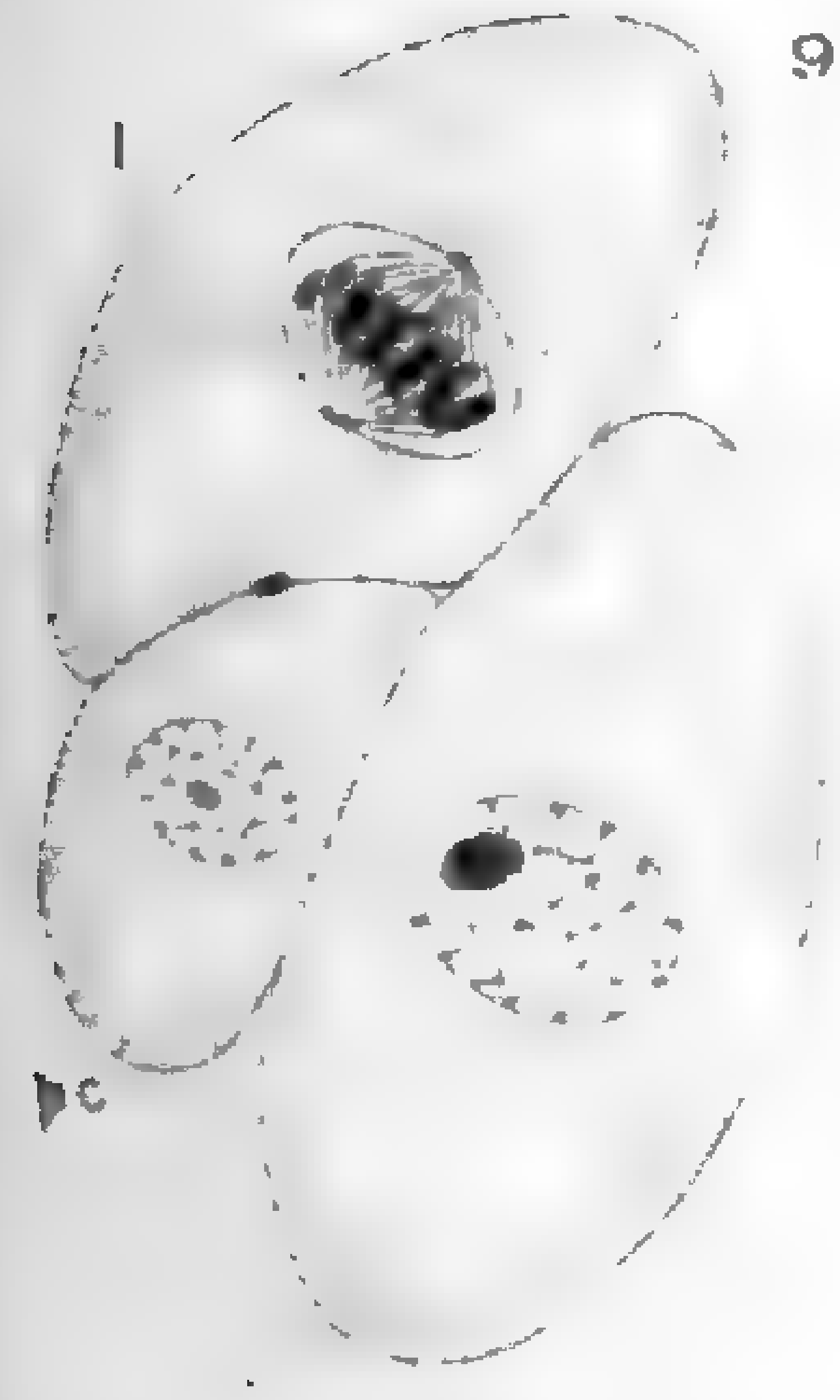

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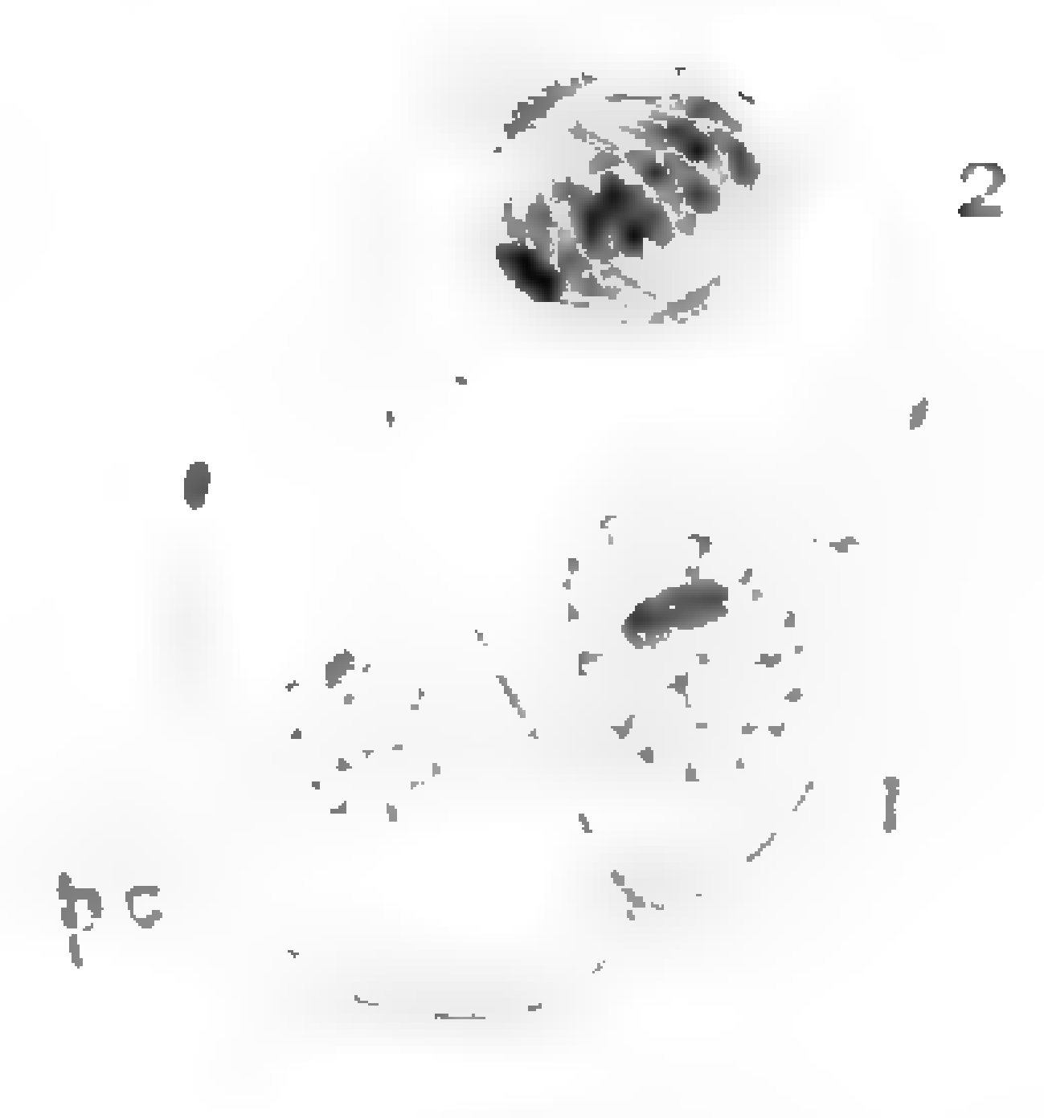

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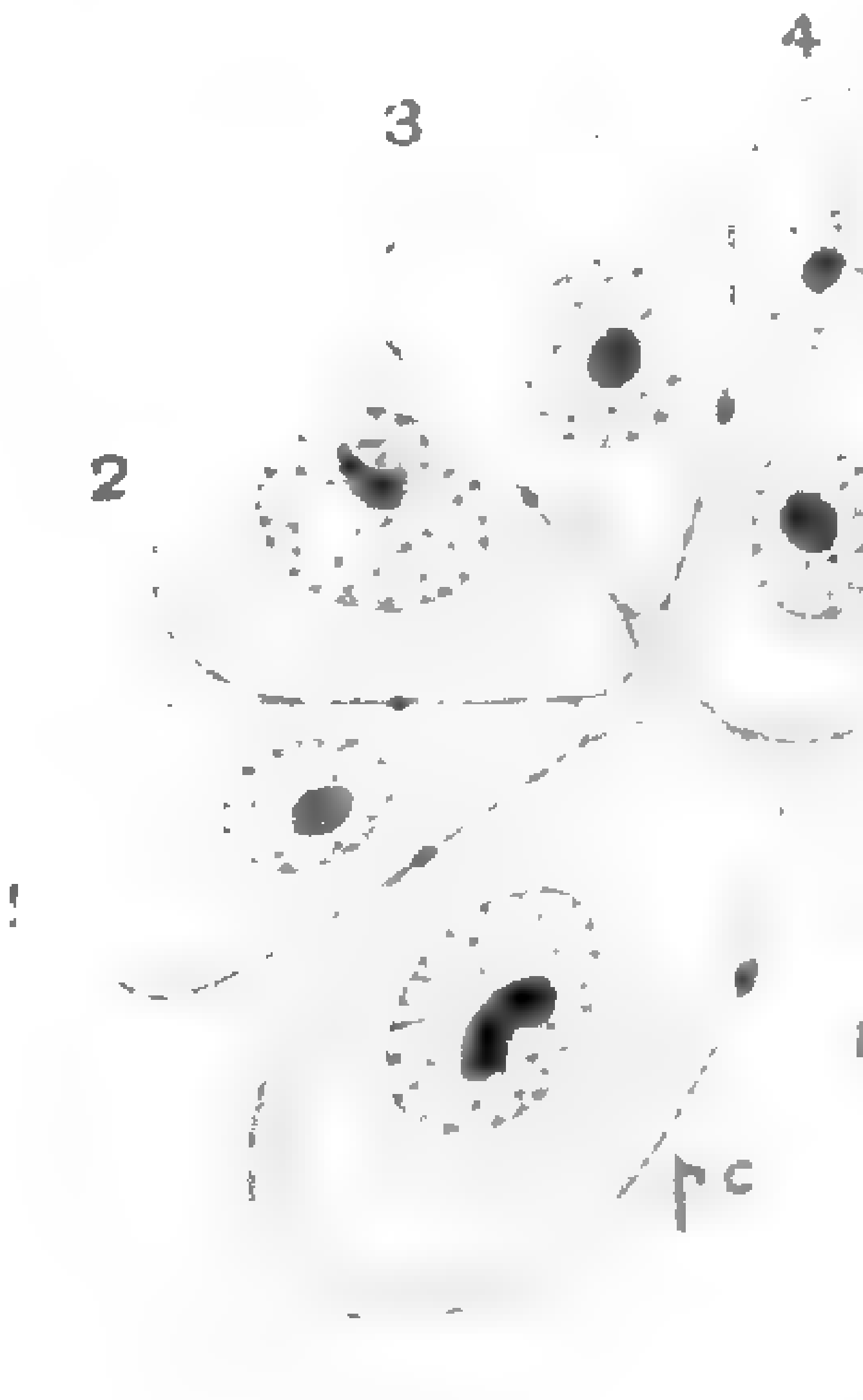

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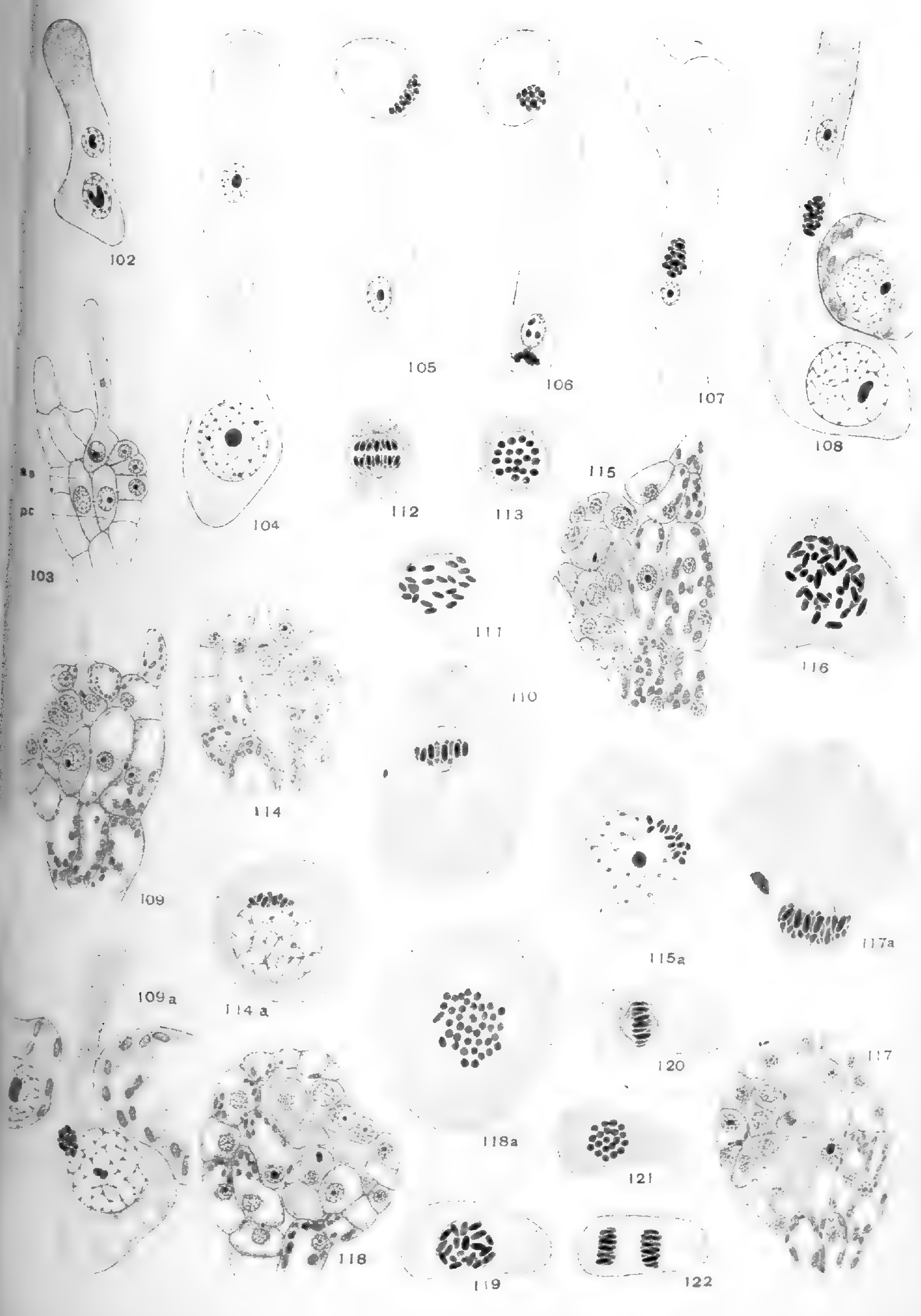

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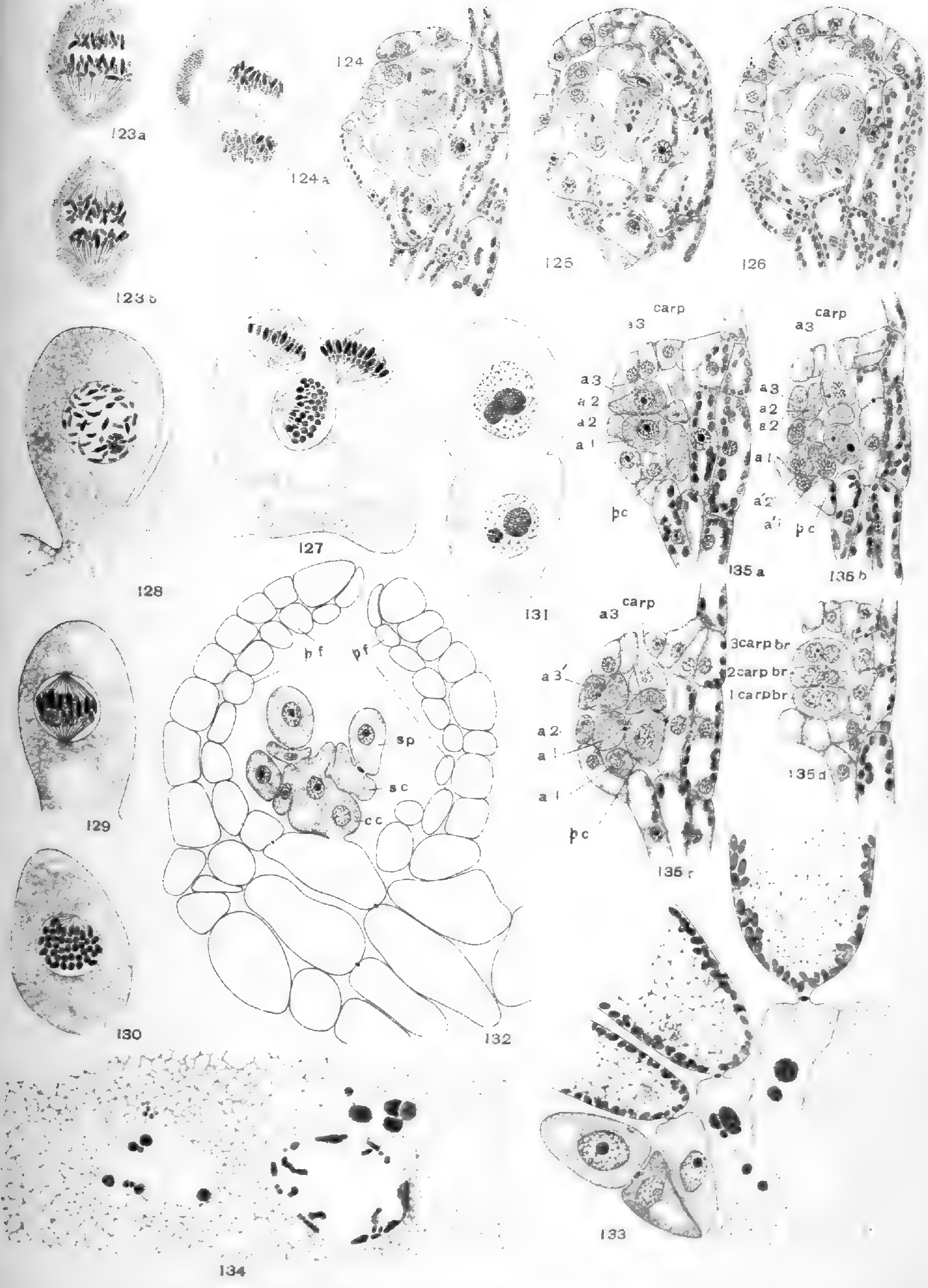

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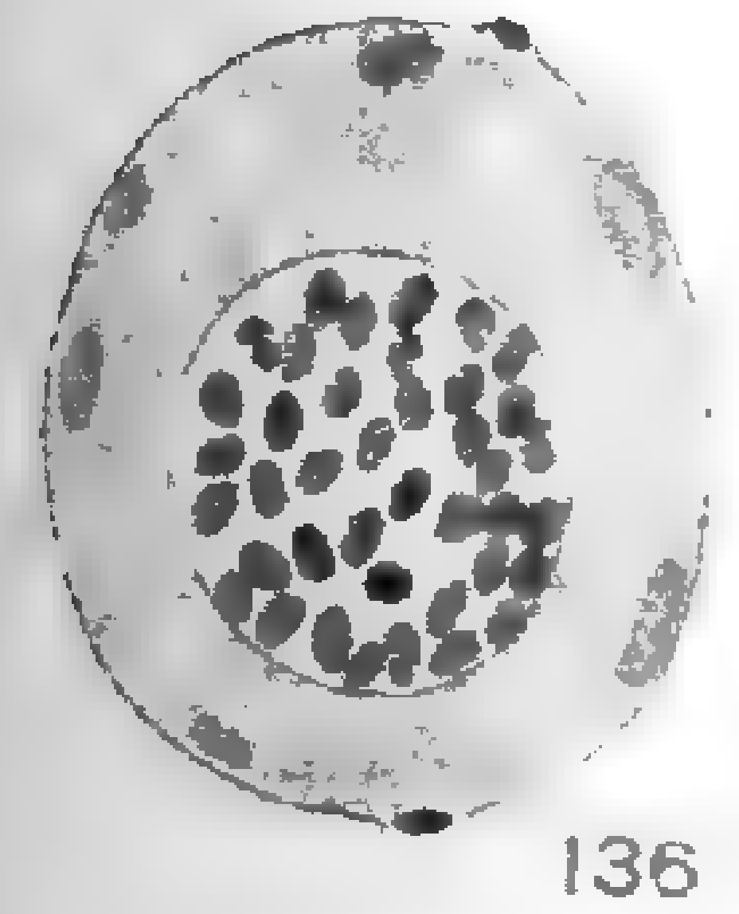
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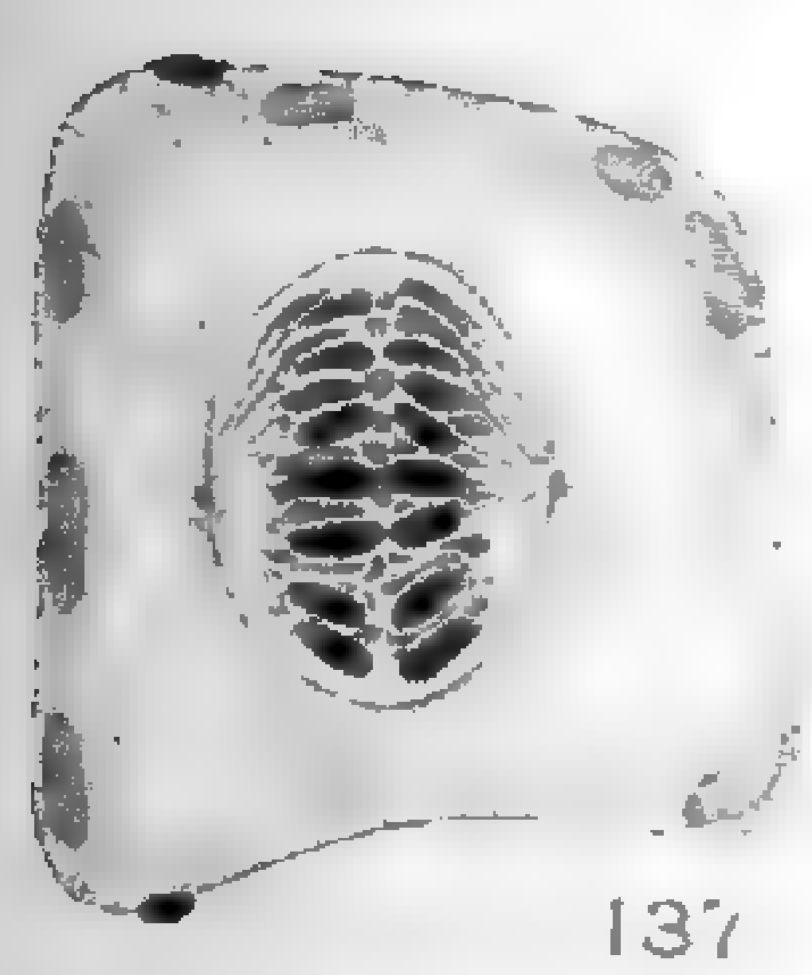
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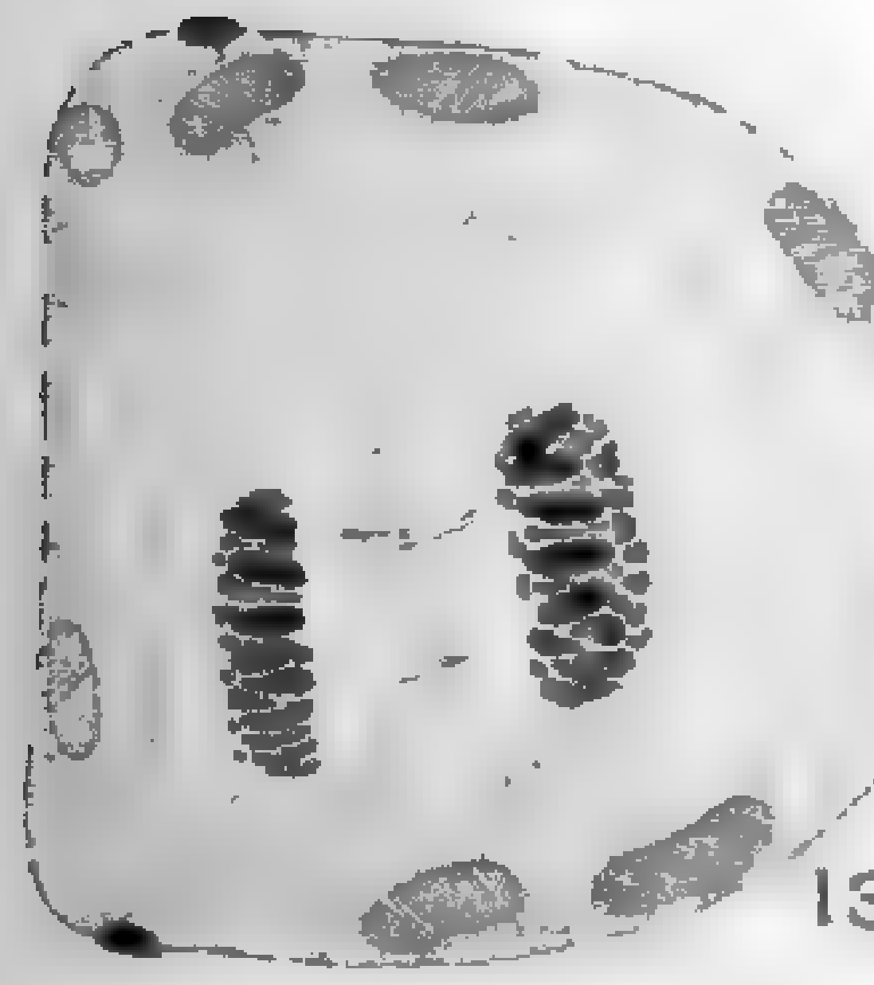
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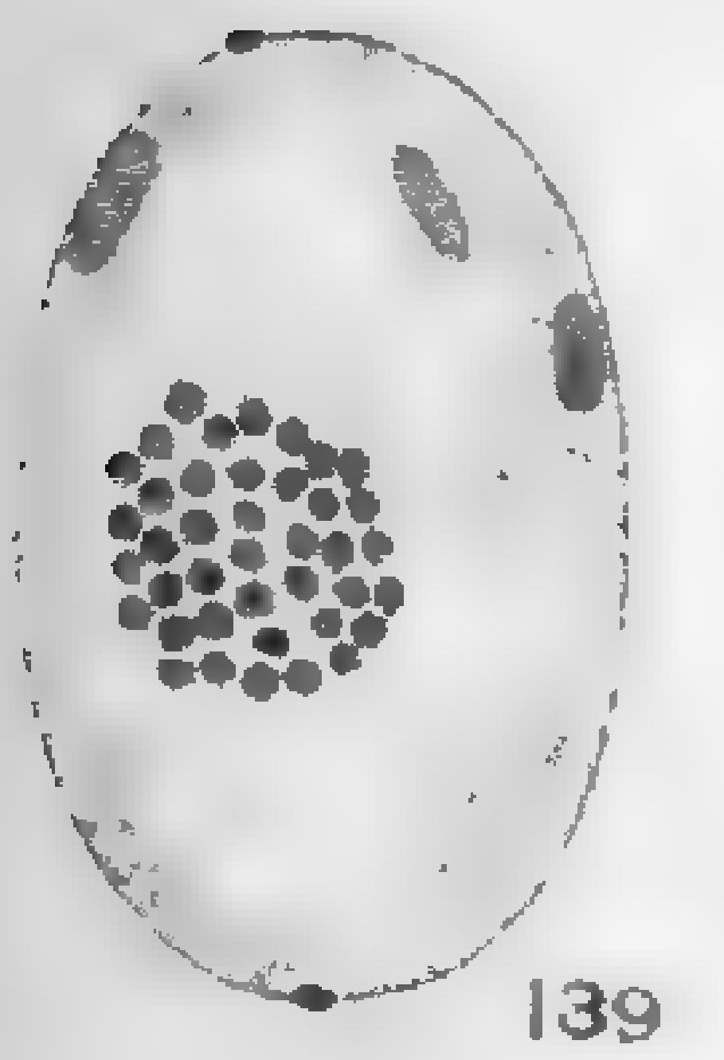
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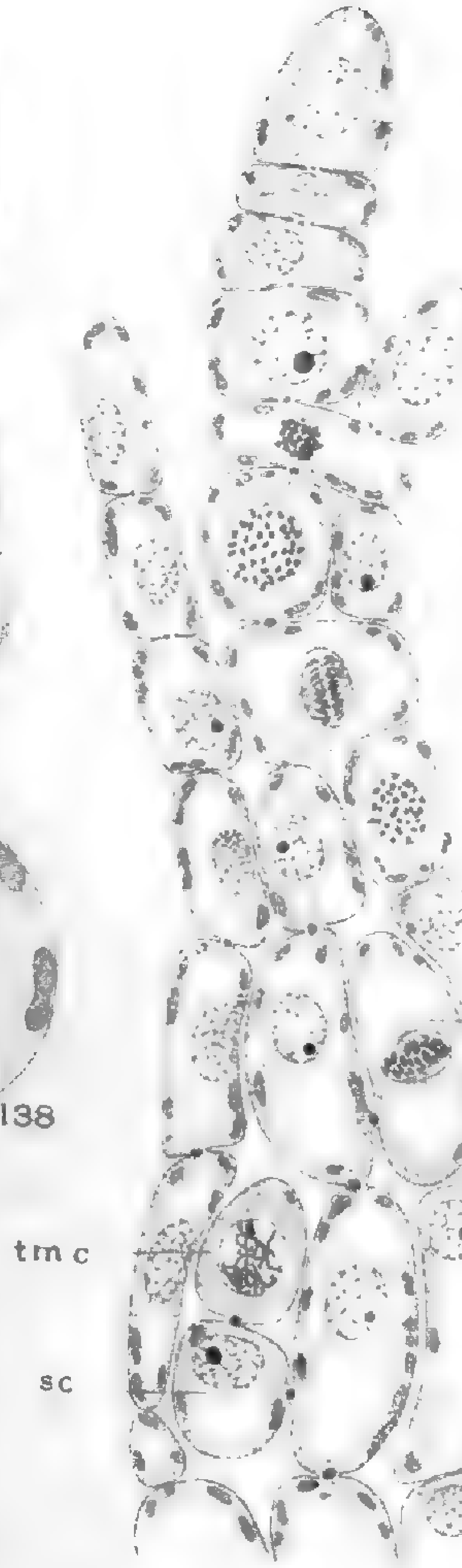

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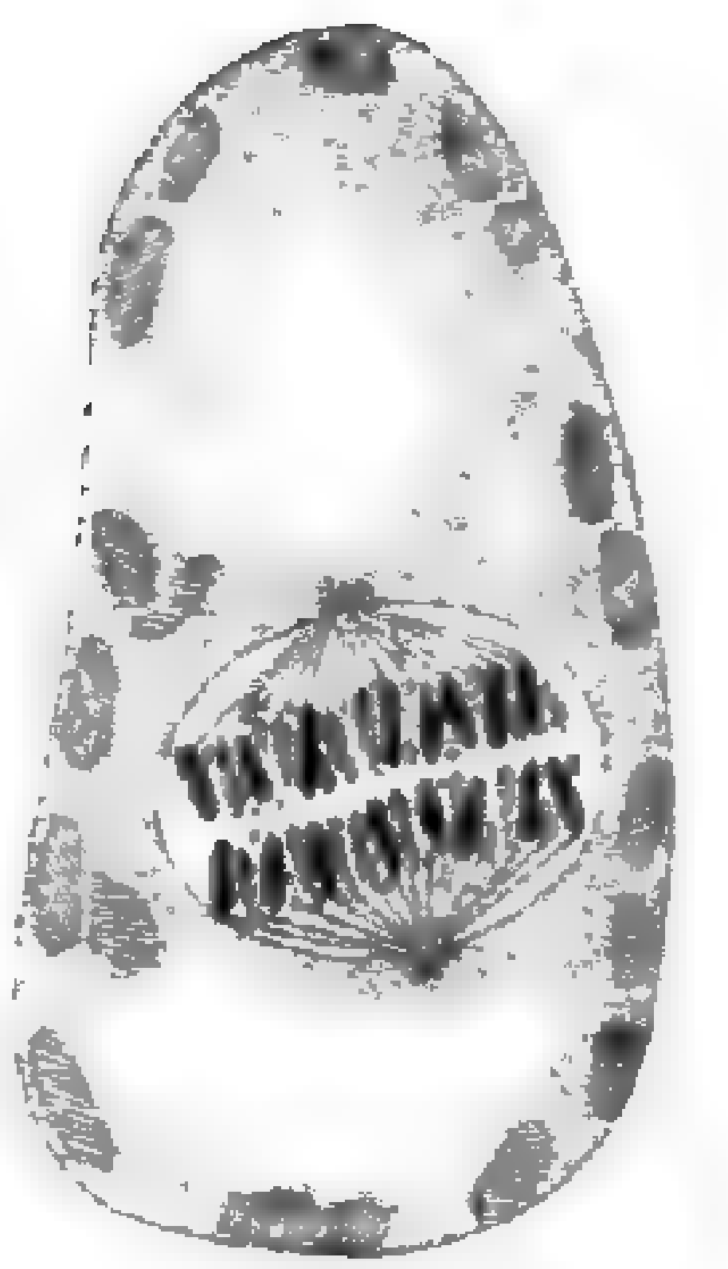
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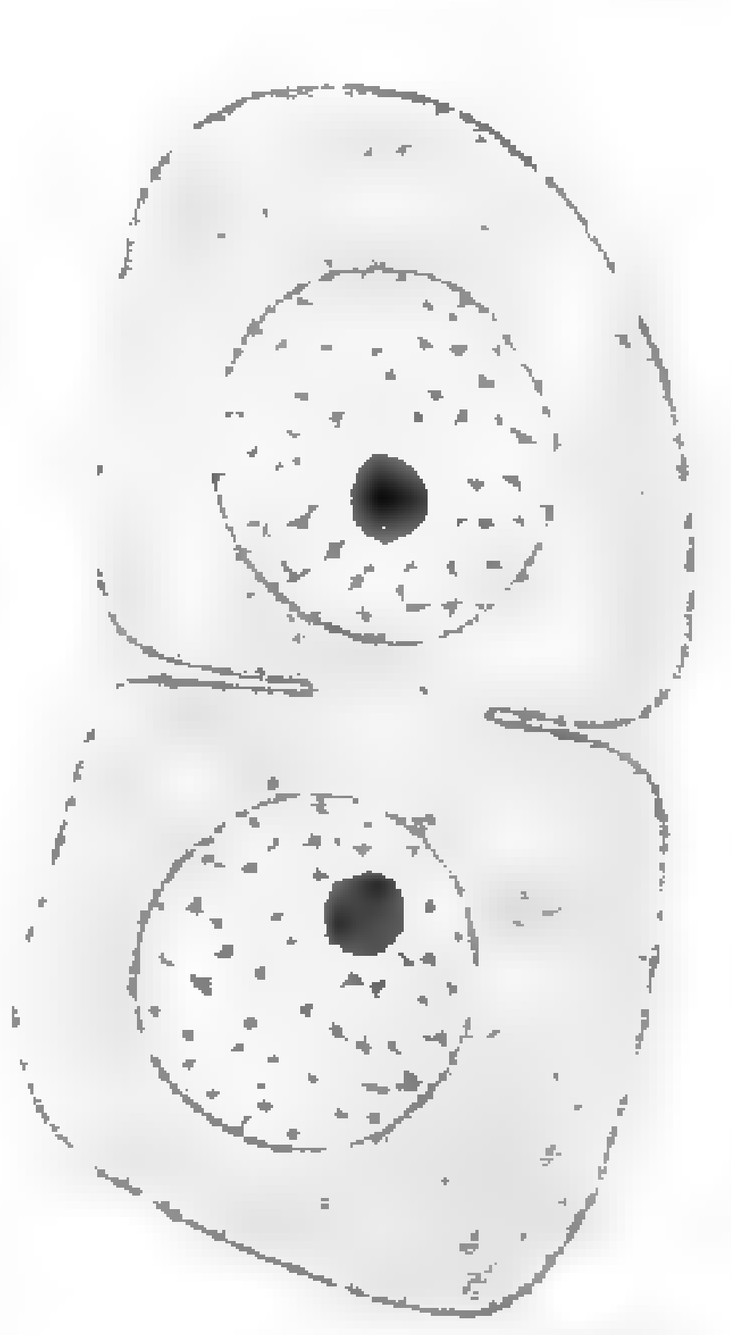
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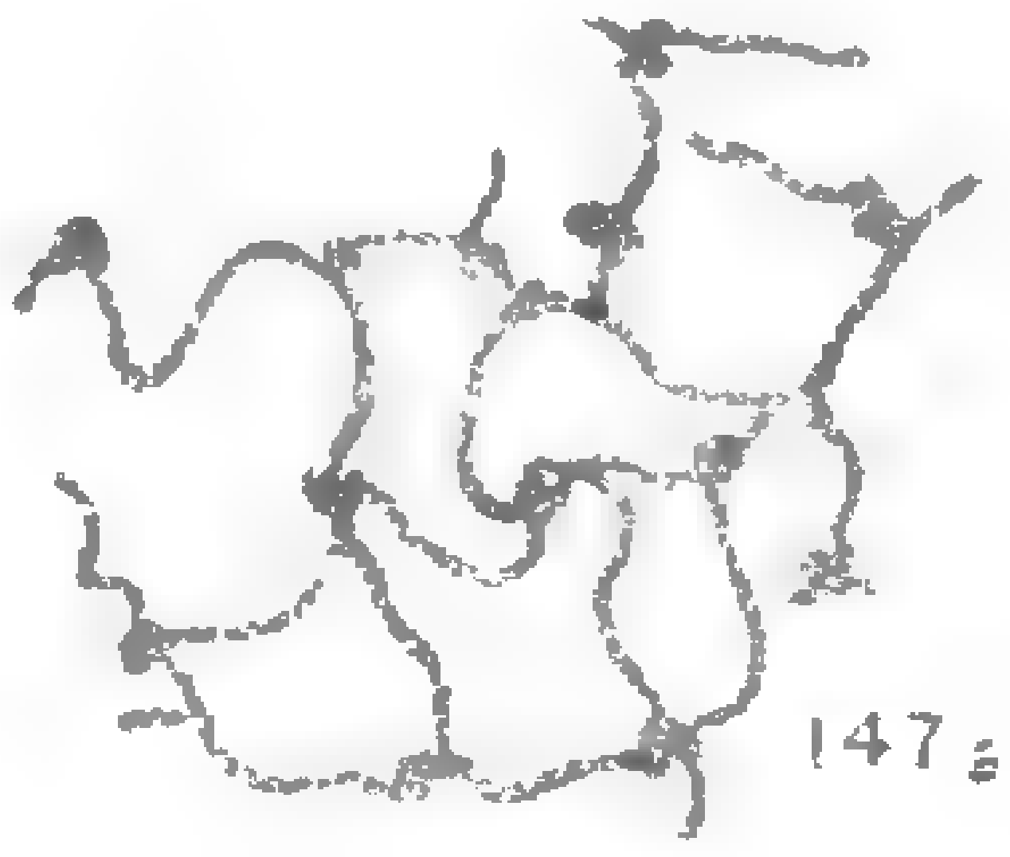
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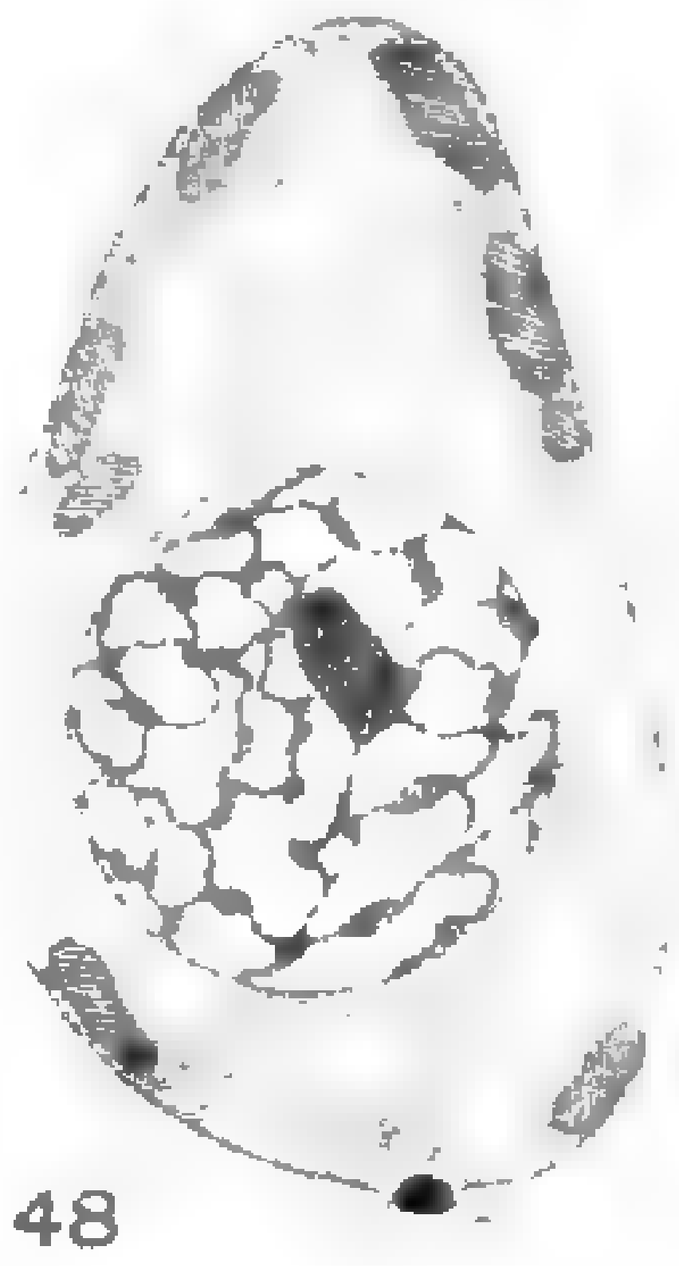
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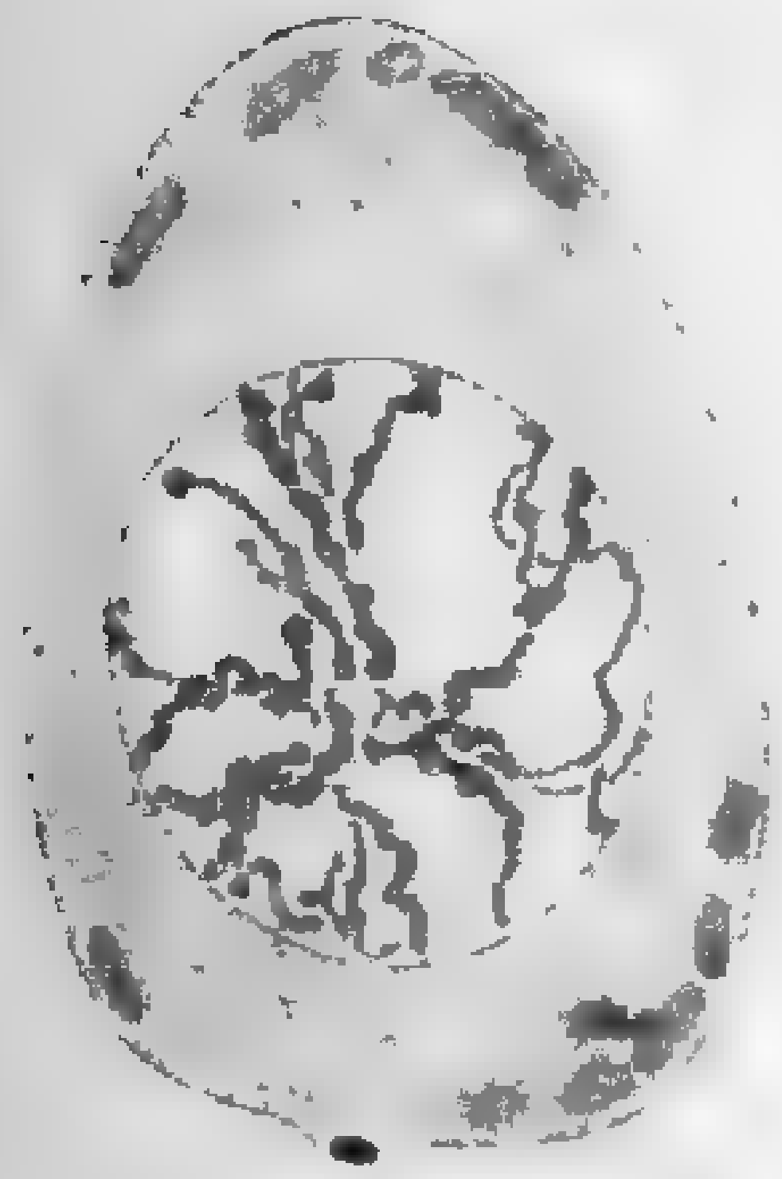
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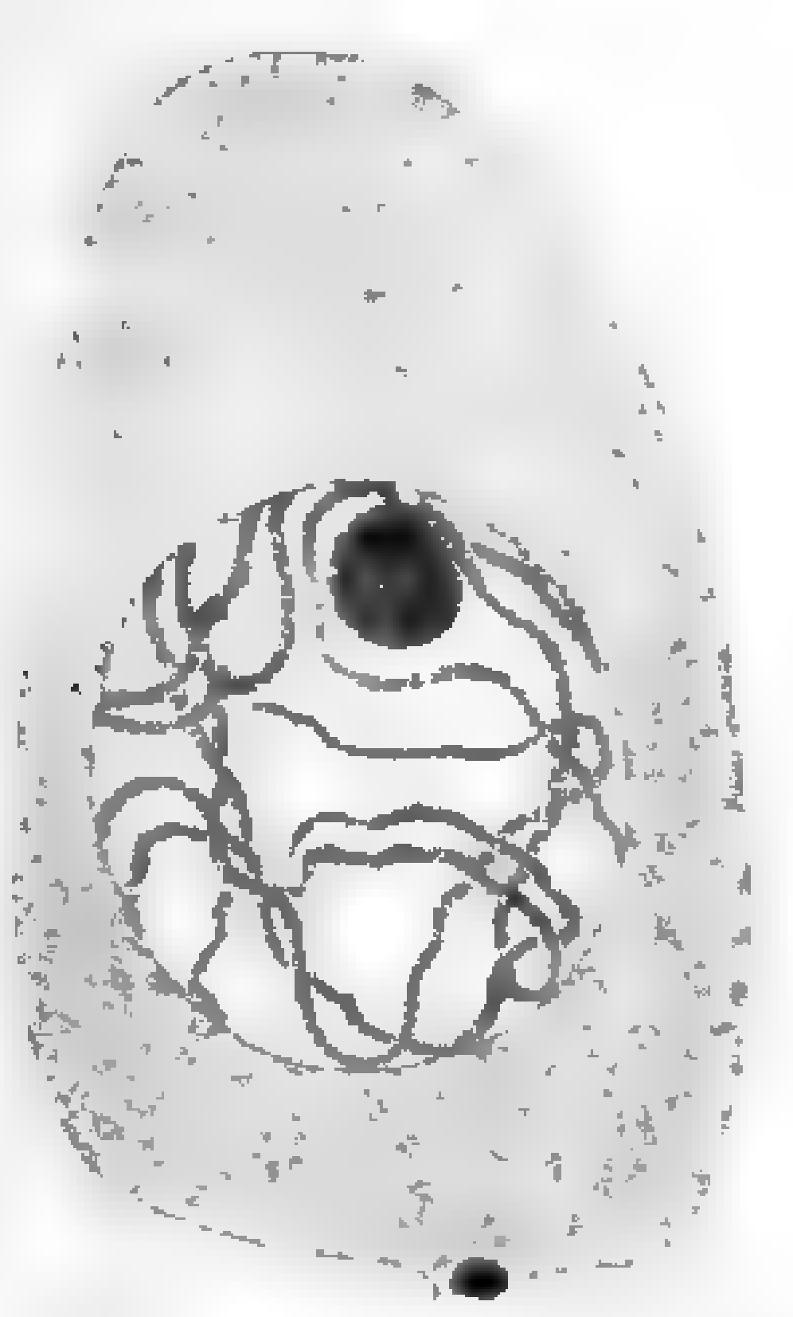
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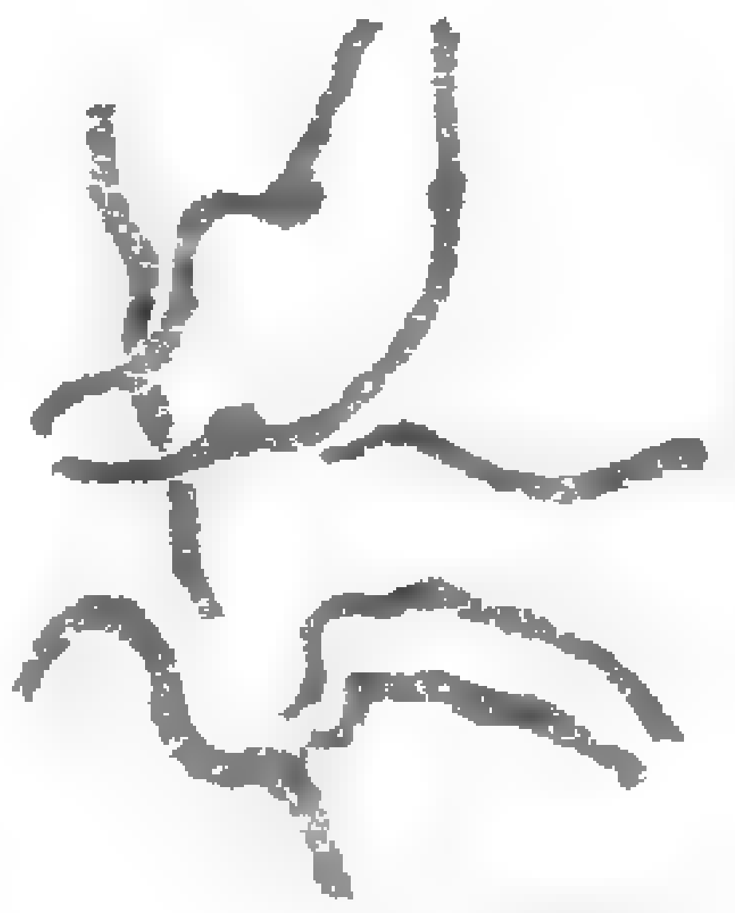
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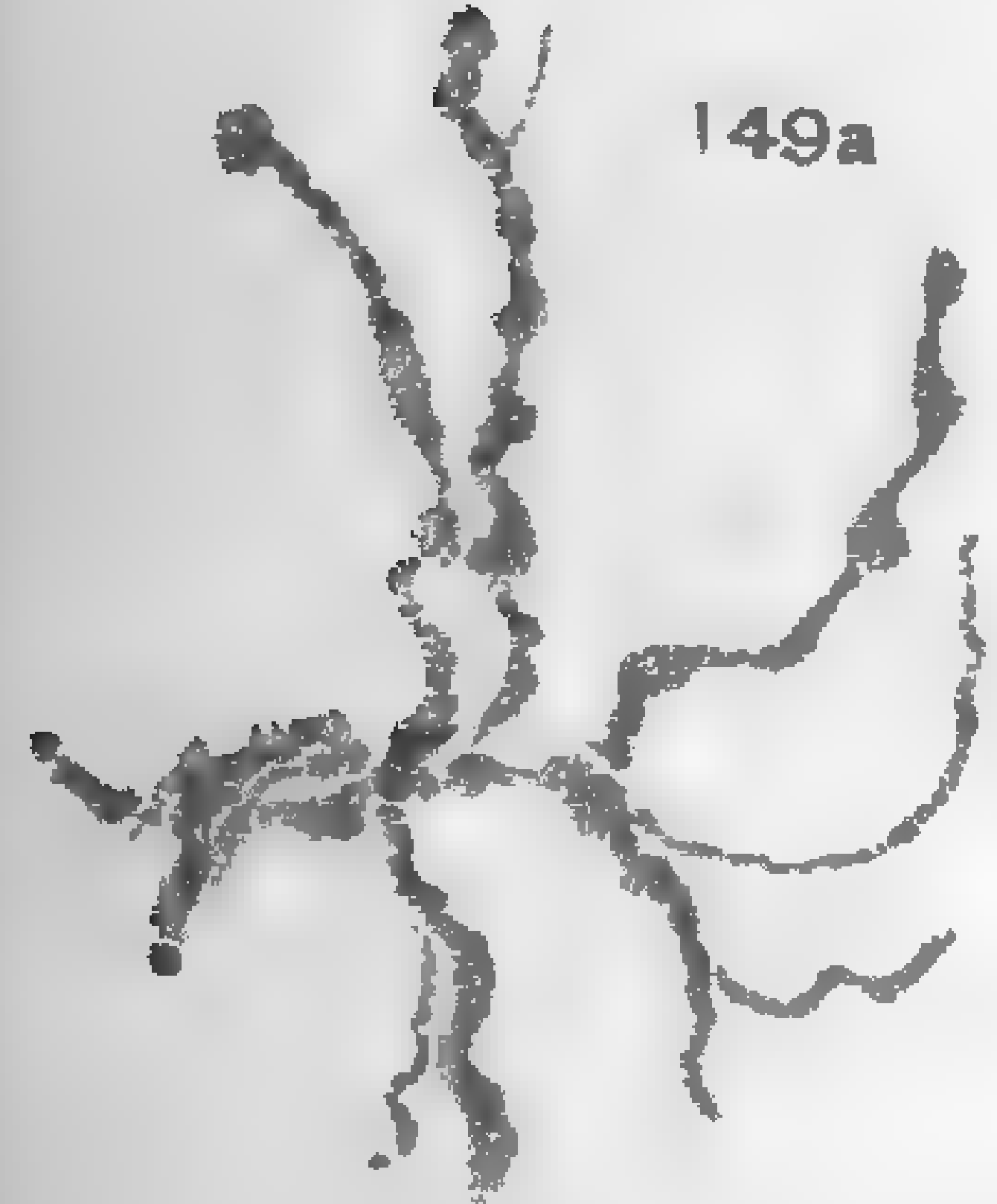
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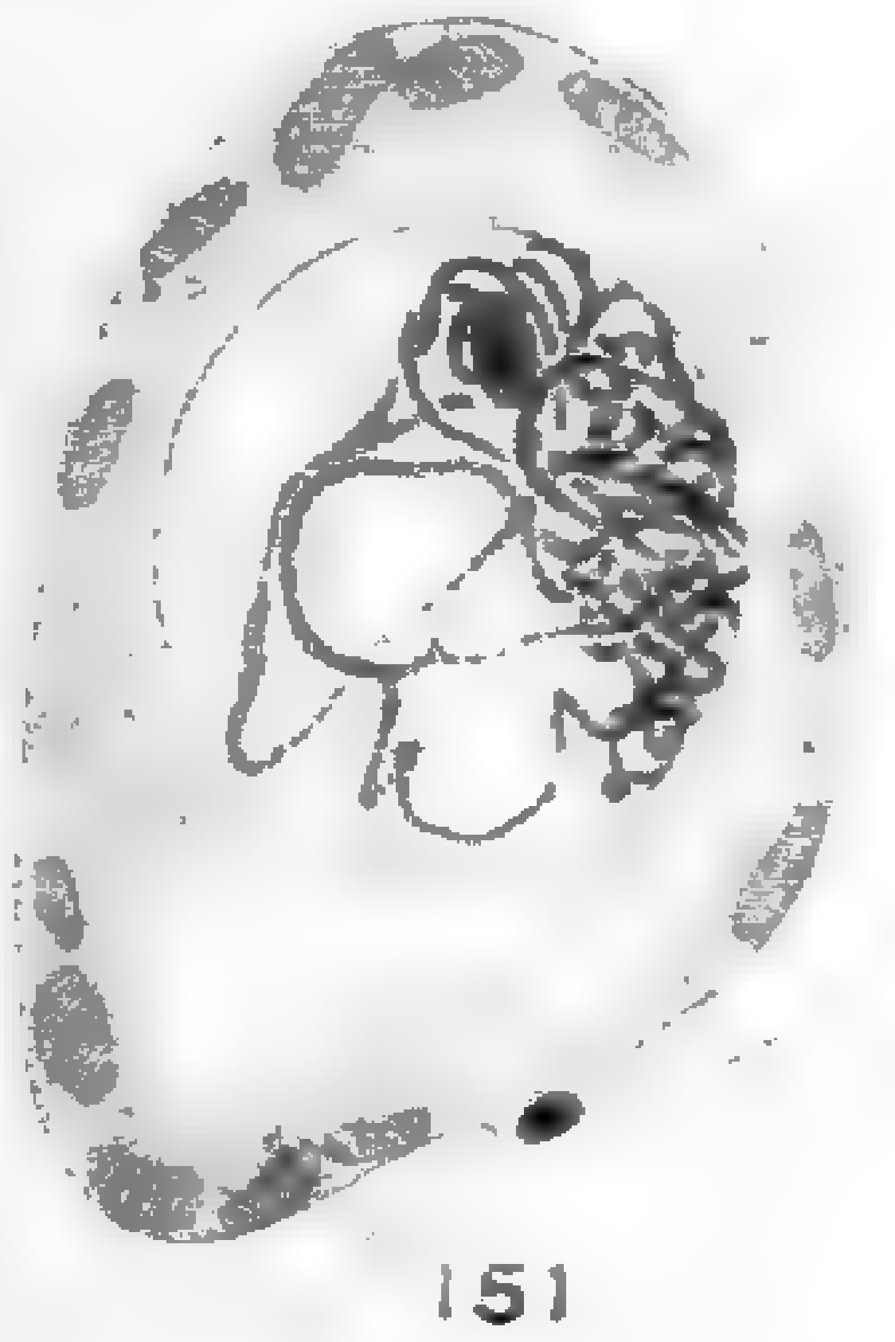
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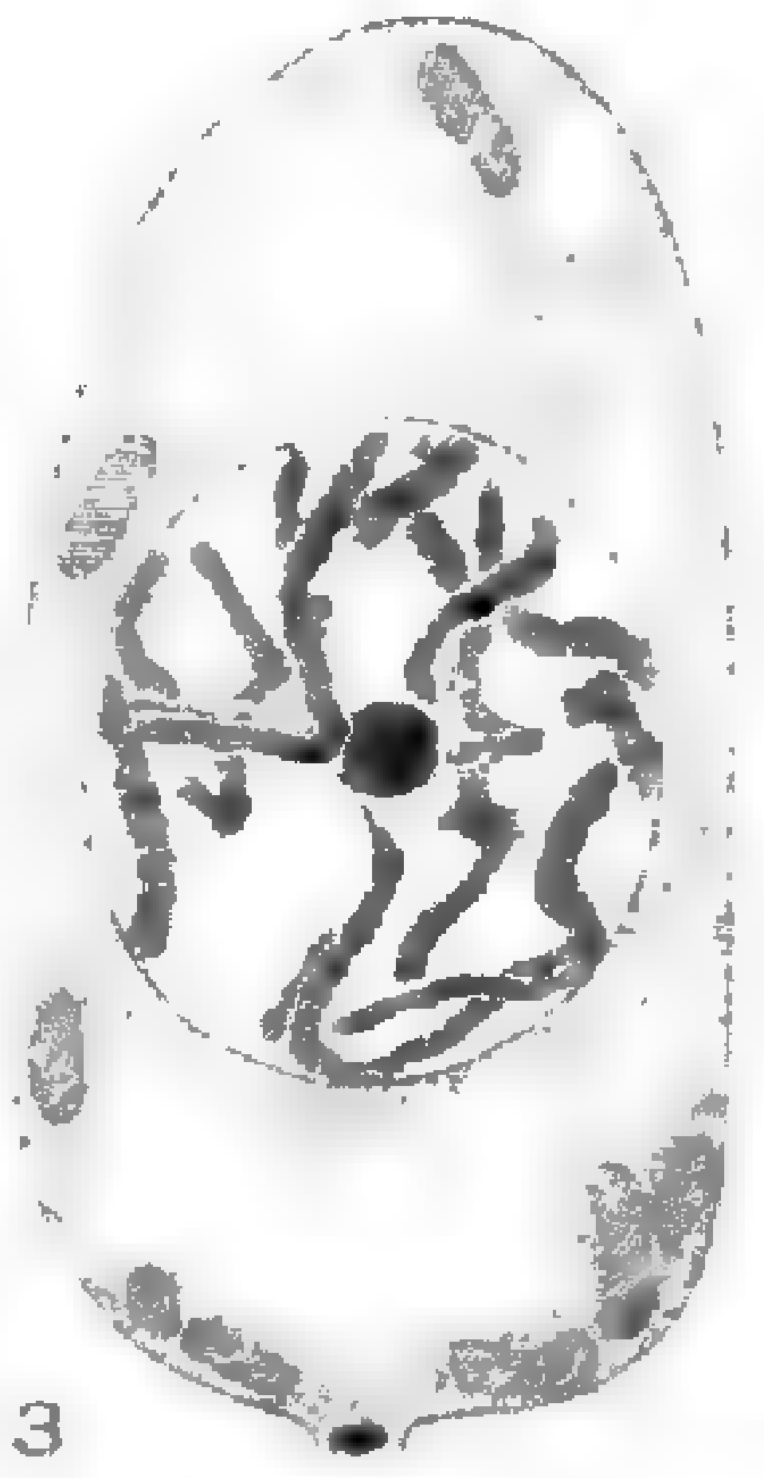
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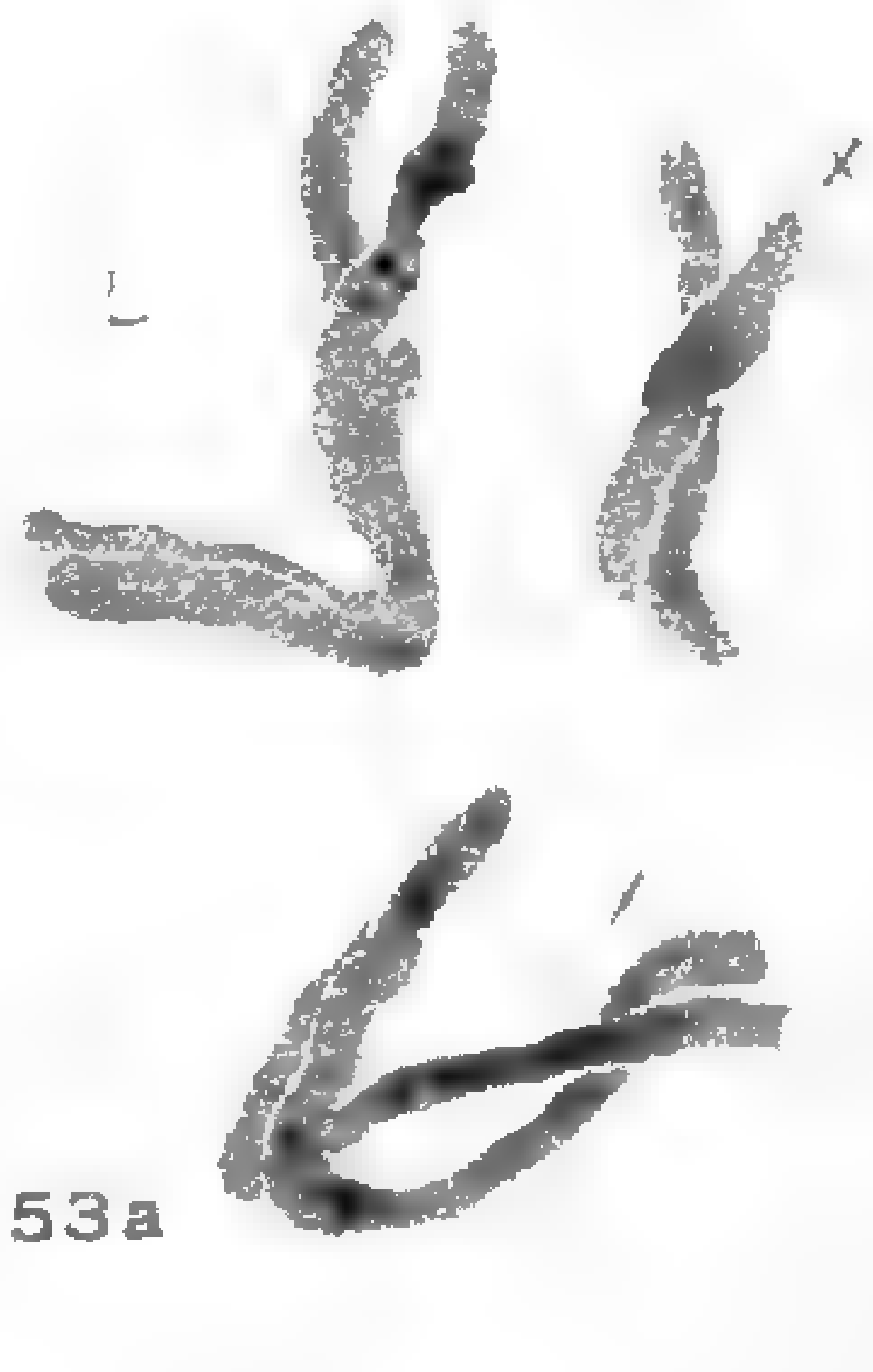
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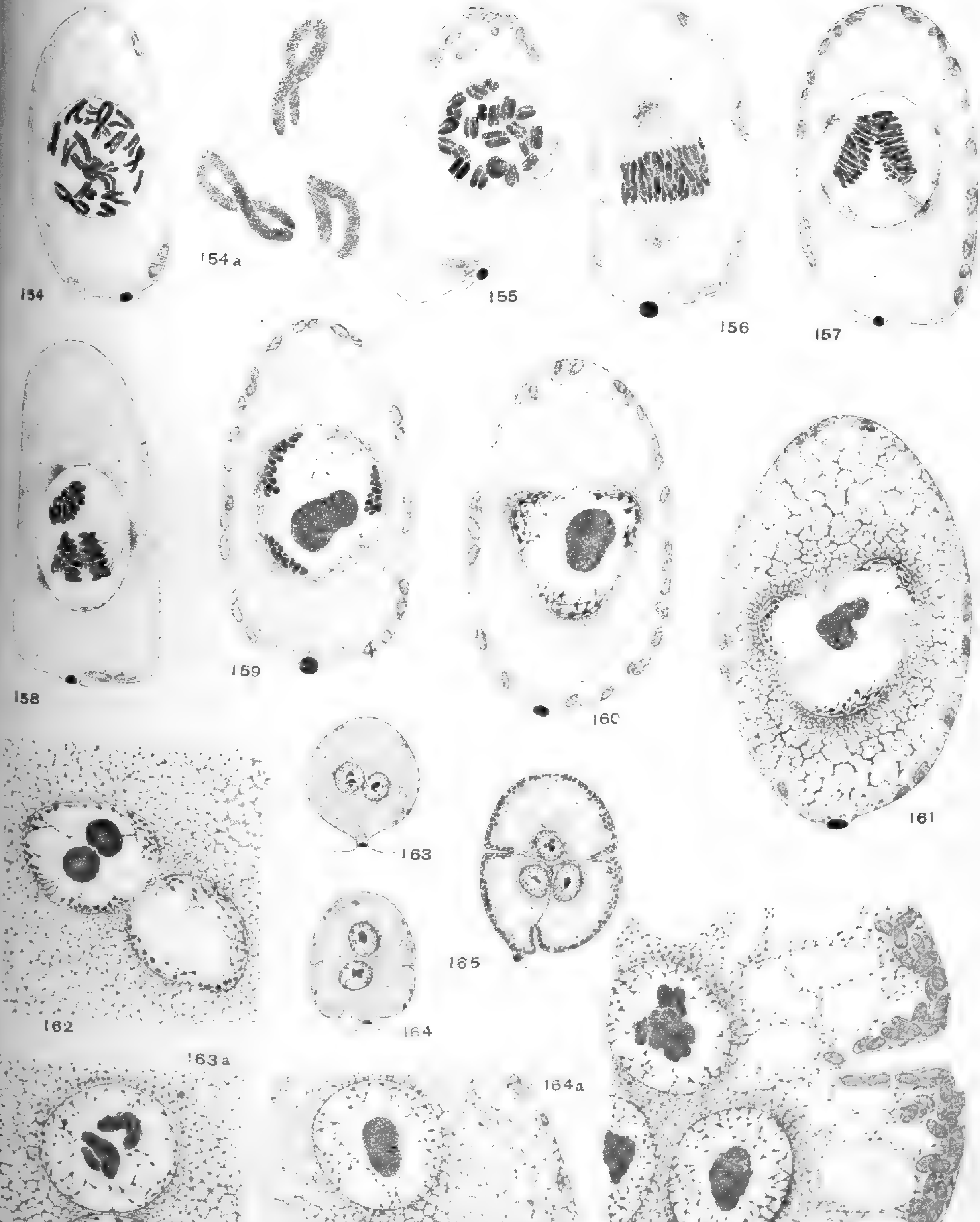

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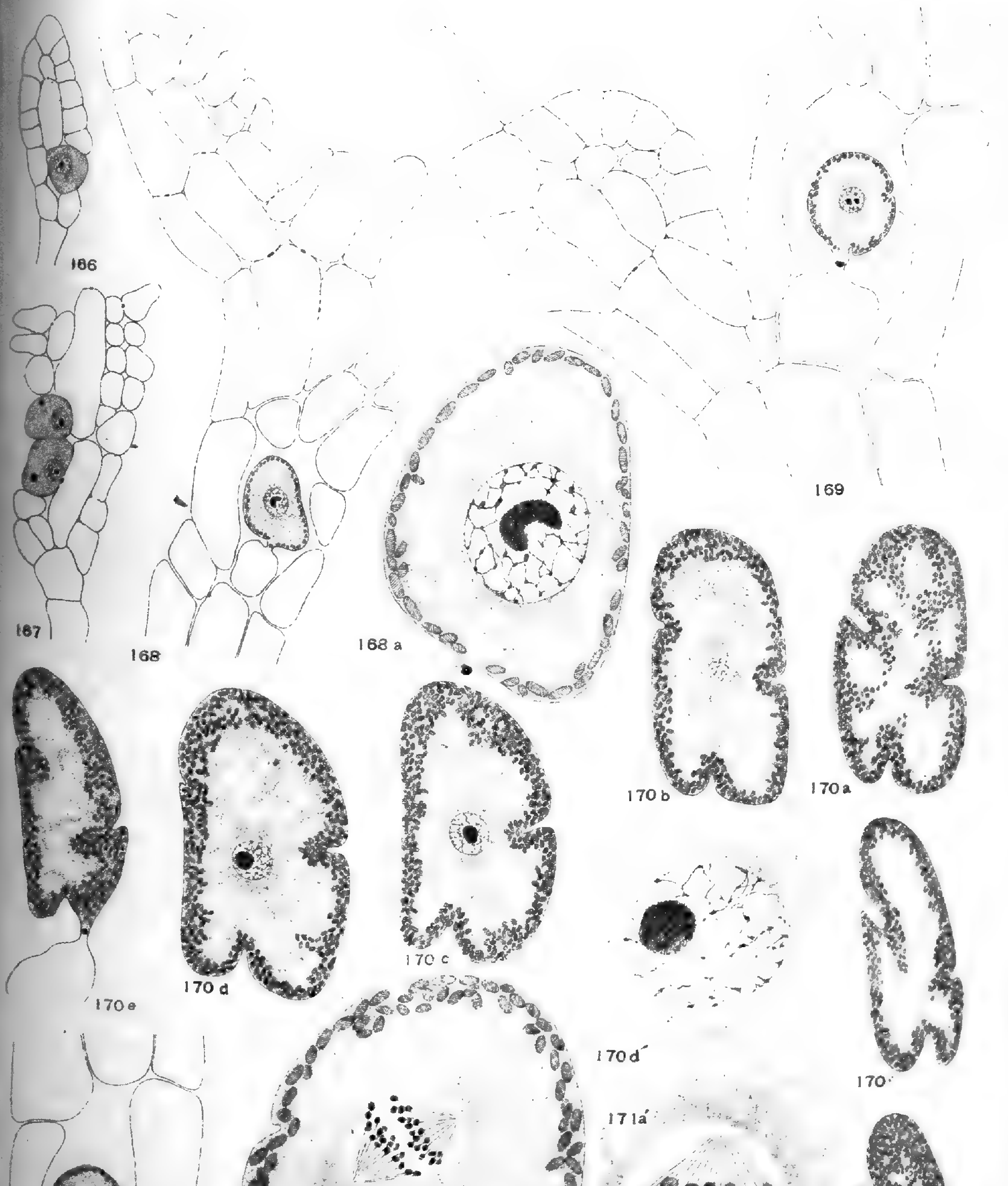

YAMANOUCHI on POLYSIPHONIA

FIG. 163a. The nuclei of *fig. 163* under higher magnification, showing their structure with linin network and nucleoli.

FIG. 164. The four daughter nuclei are completely formed (two visible); cleavage furrow appearing at the periphery.

FIG. 164a. Portion of *fig. 164* under higher magnification, showing details of cleavage furrows.

FIG. 165. Tetraspore mother cell with cleavage furrows growing towards the center.

FIG. 165a. Portion of *fig. 165* under higher magnification, showing the vacuolar structure and the progress of the cleavage furrows.

PLATE XXVIII.

Abnormalities.

FIG. 166. A young antheridium in which a stalk cell has increased in size and assumed the appearance of an auxiliary cell in the procarp.

FIG. 167. Showing the division of a stalk cell; the black spot within the cell indicates transverse section of protoplasmic strands connecting it with other stalk cells above or below.

FIG. 168. A cell formed on a sexual plant whose lineage is similar to that of the tetraspore mother cell.

FIG. 168a. This cell from *fig. 168* under higher magnification; the nucleus in a resting condition.

FIG. 169. Still later stage in the formation of this cell.

FIGS. 170a–170g. Seven sections of a similar cell; nucleus remains undivided, although the beginning of a cleavage furrow is present, which however never proceeds further.

FIG. 170d′. Nucleus of *fig. 170d* under higher magnification, in a resting condition.

FIG. 171. A rare case where the nucleus of this cell undergoes a typical mitosis.

FIG. 171a. The nucleus of *fig. 171* under higher magnification.

FIG. 171a′. The mitotic figure of *fig. 171a* under still higher magnification shows that this division is typical and that the daughter chromosomes are 20 in number in each group.

THE MORPHOLOGY OF THE ASCOCARP AND SPORE-FORMATION IN THE MANY-SPORED ASCI OF THECOTHEUS PELLETIER I.

JAMES BERTRAM OVERTON.

(WITH PLATES XXIX AND XXX)

ALTHOUGH free cell formation and spore formation have been thoroughly described by several authors, the process has not been followed in asci containing more than eight spores. In view of the old and widely held opinion that the ascus closes a sporophyte generation and is a spore mother cell, the study of the development of a many-spored ascus becomes especially important. The correlative phenomenon of the regular formation of eight nuclei in the ascus by a triple division, whether eight spores or less are to be formed, has been well established; but the variations from the typical method of spore formation and the necessary nuclear and cell divisions, by which more than eight spores are formed, are still in need of further study, and may prove valuable in aiding to solve the character of this peculiar organ. The presence of a true sexual process in the higher fungi, especially among the Ascomycetes, has been established beyond a doubt by the investigations of HARPER and others, but much still remains to be learned concerning the morphology of the sexual organs and ascogonia in the individual forms of this group.

The present investigation was undertaken during the past year, in order to determine the method of spore-formation in many-spored asci. *Thecotheus Pelletieri* presented itself as favorable material. Incidentally stages in the development of the ascocarp have been found which will also be described. The fungus agrees in general with the descriptions and figures of *Thecotheus Pelletieri* (Cr.) Boud., except that the asci are less conspicuously exserted than shown in the figures of CROUAN ('57), BOUDIER ('69), PATOUILLARD ('83), and REHM ('96), and the spores are also faintly colored. BOUDIER, to whom I have also sent material, has had the kindness to examine the fungus and has confirmed the determination, with the note, however, that he finds the spores somewhat larger than in the type.

As will be seen from the description below, the form differs from the species of Ryparobius described by BARKER (**:03**, **:04**) in having several ascogonia instead of a single one. As it may be found that this is a character of generic significance, I have thought best to follow BOUDIER in including this form under a separate generic name.

The investigation of the Ascomycetes has shown that there are great variations in the morphology and development of both fruit bodies and reproductive organs, and a sharp distinction may be made as to whether the sexual organs, associated with ascocarp formation, occur singly or in groups. Below I have brought together those forms whose fruit bodies develop from a single ascogonium, as contrasted with those whose ascocarps develop from several ascogonia. In strong contrast to these may also be added a third group of apparently apogamous forms, whose fruit bodies develop directly from a cell of the mycelium without the appearance of sexual organs.

I. In the following forms the ascocarps develop in connection with a single set of sexual organs: Monascus (BARKER **:03**, OLIVE **:05**), Dipodascus (JUEL **:02**), Gymnoascus (BARANETZKY **'72**, VAN TIEGHEM **'76**, **'77**, EIDAM **'83**, Miss DALE **:03**), *Erysiphe cichoracearum* (*Sphaerotheca castagnei*) (DEBARY **'63**, HARPER **'95**), *Erysiphe galeopsidis* (DEBARY **'70**), *Erysiphe communis* (DEBARY **'70**, HARPER **'96**), *Sphaerotheca humuli* (BLACKMAN & FRASER **:05**), *Phyllactinia corylea* (HARPER **:05**), perhaps *Eurotium repens*, *Aspergillus glaucus*, (DEBARY **'70**), *Penicillium glaucum* (BREFELD **'74**), *Aspergillus glaucus* (VAN TIEGHEM **'77**), Chaetomium (VAN TIEGHEM **'75**, **'76**, EIDAM **'83**, ZUKAL **'86**, OLTMANNS **'87**), *Stictosphaeria Hoffmanni*, with several species of Diatrype, Eutypa, Quaternaria, and Xylaria (FUISTING **'67**), *Sphaeria lemaneae*, *Sordaria fimiseda* (WORONIN **'70**, GILKENET **'74**), and *Ceratostoma brevirostre*, *Hypocopra* sp. (Miss NICHOLS **'96**). Among the Discomycetes the following investigated forms show a single ascogonium: *Ascobolus furfuraceus* (JANCZEWSKI **'72**, HARPER **'96**), *A. pulcherrimus* (WORONIN **'66**), *Ryparobius* sp. (BARKER **:03**, **:04**), *Peziza granulosa*, *Lachnea scutellata* (WORONIN **'66**), *Humaria granulata* (BLACKMAN & FRASER **:06**), *Ascodesmis nigricans* (VAN TIEGHEM **'76**), and *Thelebolus stercoreus* (RAMLOW **:06**).

II. *Pyronema confluens* (TULASNE **'66**, DEBARY **'63**, KIHLMAN **'83**, HARPER **:00**), several species of Collema (BAUR **'98**), *Parmelia* *acetabulum* (BAUR :01, :04), *Anaptychia ciliaris*, *Lecanora subfusca*, *Endocarpon miniatum*, *Gyrophora cylindrica*, *Cladonia pyxidata* (BAUR :04), *Pertusaria communis*, *Pyrenula nitida* (BAUR :01), and *Boudiera Clausseni* (CLAUSSEN :05) represent the only forms thus far described in which the ascocarp is developed in connection with several ascogonia. As described below, Thecotheus also possesses a compound ascogonial apparatus from which the fructification originates.

III. In certain Pyrenomycetes ascocarp formation is apparently independent of sexual organs, being initiated by the formation of a parenchymatous mass of tissue, which is formed by the division of a single hyphal cell of the mycelium, as in Teichospora and Teichosporella (Miss NICHOLS '96) and also in Pleospora (BAUKE '77).

From the above list, selecting the best investigated forms which have a simple ascocarp, we find Dipodascus, Thelebolus, Gymnoascus, Sphaerotheca, Erysiphe, Phyllactinia, Ryparobius, Ascobolus, Humaria, and Monascus. Those having a compound apothecium are several species of lichens (in which, according to BAUR, several hundred carpogonia in some cases may be present in a single apothecium), Pyronema, Boudiera, and Thecotheus.

JUEL (:02) has studied the nuclear phenomena in Dipodascus. The sexual organs arise as short outgrowths of two neighboring cells, each gamete containing several nuclei. After the organs fuse, the walls between break down and the nuclei of the antheridium pass into the oogonium, which grows into a single ascus containing a large fusion nucleus and several smaller nuclei. Although JUEL was unable to make out the details of spore delimitation, he claims that the appearance of the cytoplasm indicates that the spores are formed by free cell formation about the descendants of the fusion nucleus, while the remaining nuclei, which did not fuse in the oogonium, lie scattered in the epiplasm. The actual process of nuclear fusion was not observed.

Miss DALE (:03) describes a sexual fusion of gamete cells in *Gymnoascus Reessii* and *G. candidus*. The oogonia and antheridia are of more or less separated origin. BARKER (:03), IKENO (:03), KUYPER (:04, :05), and OLIVE (:05) have investigated Monascus. BARKER'S and OLIVE'S accounts differ somewhat from that of IKENO. These two authors describe the ascogenous hyphae of Monascus as arising from an oogonium which has been fertilized by an antheridium, thus establishing a sexual process for Monascus. They also hold that the asci arise from the cells of ascogenous hyphae; while IKENO asserts that there are no ascogenous hyphae, but that uninucleate spore mother cells arise by free cell formation, which in turn form spores also by free cell formation. KUYPER denies any fusion of sexual cells in Monascus, mainly confirms IKENO'S observations, and regards the spore mother cells as true asci.

Two forms closely related to Thecotheus in that they belong among the Ascobolaceae have been investigated. BARKER (:**03**, :**04**) in two preliminary notes has described the presence of sexual organs in Ryparobius. The development of the ascocarps was observed step by step under the microscope in hanging drop cultures. The archicarp consists of a small coiled oogonium and a slender antheridium arising from the next cell of the mycelium, growing out over the tip of the oogonium, and fusing at the point of contact. Both antheridium and oogonium are uninucleate when first formed, but subsequently nuclear division occurs in each organ. Nuclear fusion probably occurs, constituting a regular fertilization, although this process was not actually observed. Walls are formed, so that the resulting cells are uninucleate with the exception of the penultimate cell of the ascogonium, which is sometimes found to contain two nuclei lying close together. It will be seen that there is great similarity between Ascobolus and Ryparobius as to the morphology of both the ascogonia and the ascocarps. The ascogenous hyphae, however, do not originate from any particular cell of the ascogonium, as has been described for Ascobolus.

CLAUSSEN (:**05**) has also worked out the morphology of the ascocarp of a form which he at first believed to be *Boudiera hyperborea*, but which HENNINGS (:**03**) described as a new species under the name of *B. Clausseni*. CAVARA (:**05**), basing his conclusions upon CLAUSSEN'S figures, descriptions, and culture methods, believes that this fungus is not a new species of Boudiera, as HENNINGS has described, but that it corresponds perfectly to a species of Ascodesmis, which has been described by VAN TIEGHEM ('**76**) and later by ZUKAL ('**86**). VAN TIEGHEM described in detail two species, *A. nigricans* and *A. aurea*. CAVARA believes that the fungus is *A. nigricans*

Van Tiegh., and that it has been found by him ('89) in the neighborhood of Pavia. DANGEARD (:03) has also briefly described the development of *A. nigricans*, which CAVARA fails to note. So far as I am able to judge from the figures and descriptions of these authors, I see no reason for doubting that CLAUSSEN'S fungus represents a new species of Boudiera, as described by HENNINGS. CLAUSSEN grew the fungus on cultures and was able to trace the life history from spore to spore. He found that the archicarps consisted of antheridia and oogonia spirally coiled together and borne in groups. As in Pyronema, the apothecium originates from several pairs of gametes. The ascogenous hyphae appear to originate from any or all of the cells of the ascogonium.

The latest work of HARPER (:05), already referred to, traces the formation of the sexual organs and nuclear fusion in *Phyllactinia corylea* in the minutest detail, showing that the ascocarps develop as the result of fertilization.

BLACKMAN and FRASER (:06) point out that the non-cytological investigation of several forms has shown that a normal sexual process is not to be expected in all, and they have therefore undertaken the cytological investigation of *Humaria granulata*, a form in which no antheridium is present. They find that the oogonium develops as a side branch from multinucleate cells of the mycelium, but that no antheridia are formed as described by WORONIN ('66). The archicarp consists of a varied number of cells, the apical cell of which is much swollen and vacuolate, becoming the ascogonium. Investing hyphae arise from the stalk cells but no antheridia are developed. The ascogonial cell contains a number of nuclei probably formed by division of its primary nuclei. These female nuclei fuse in pairs, thus constituting what they regard as a reduced sexual process, similar to what occurs in the development of the aecidium of *Phragmidium violaceum*. This vegetative fusion occurs in the ascogonia of various ages, and at no definite stage as in Pyronema. These fusion nuclei pass into the ascogenous hyphae, and on account of their size are easily distinguished from those of the vegetative hyphae.

RAMLOW (:06) has shown that the archicarp of *Thelebolus stercoreus* arises as a much twisted uninucleate organ from the uninucleate cells of the mycelium. No antheridium is developed, but the nucleus of the oogonium divides by successive division until eight free nuclei are formed. Cross walls are then formed in such a manner that one cell contains two nuclei. This cell is larger and finally develops a single ascus, as in Sphaerotheca. No reduced sexual fusion, such as described by BLACKMAN and FRASER, was observed, and RAMLOW believes that Thelebolus is strictly apogamous. Although this form has been placed among the Hemiasci by several earlier authors, RAMLOW from his studies believes it to be a member of the Ascobolaceae, as suggested by SCHROETER and REHM.

That a sexual reproduction occurs in the lichens, comparable to that found in the red algae, as first described by STAHL (**'77**), and confirmed by BORZI (**'78**) for other species of Collemaceae, has been practically established by the investigations of several later authors. Although KRABBE'S work (**'83, '91**) on Cladonia, Baeomyces, and Sphyridium would indicate that sexual organs were absent in these forms, yet WAINIO (**'90, '97, '98**) claims to have found trichogynes in very young podetia of Cladonia, which would show that sexual organs are present. BAUR'S work (**'98**) on *C. crispum* confirms STAHL'S observations in every detail. He figures and describes carpogonia and trichogynes. His work also shows that fertilization is a necessity to the development of asci. If the carpogonia are not fertilized by a spermatium, they develop vegetative hyphae; while each cell of the carpogonium which has been fertilized develops ascogenous hyphae. The discovery by STAHL and LINDAU (**'88**) of trichogynes in *Physcia pulverulenta* has been confirmed by DARBISHIRE (**'99**), who finds a trichogyne and a carpogonium, each cell of which is uninucleate. The cells of this carpogonium become connected so as to form a more or less continuous structure. LINDAU (**'88, '89**) has also described the presence of trichogynes in several other species of lichens, but denies that they are sexual organs. In a more recent work BAUR (**:01**) finds that *Parmelia acetabulum*, *Anaptychia ciliaris*, *Pertusaria communis*, and *Pyrenula nidia* have carpogonia. Anaptychia possesses a single carpogonium, while the other forms have the carpogonia in groups, thus making the fruit body a compound apothecium. BAUR'S opinion is that fertilization occurs by means of spermatia combining with the trichogynes. In a still more recent work BAUR (**:04**) finds the ascogenous hyphae of Parmelia, Anaptychia, Endocarpon, Gyrophora, Lecanora, and Cladonia arising from carpogonia similar to those of Collema, so that these forms also probably possess sexual organs. Solorina is probably apogamous, behaving in this respect like *Peltigera peltidea* and Nephromium as described by FÜNFSTÜCK (:**02**), in which trichogynes have disappeared. SCHULTE (:**04**) has studied the structure of several species of Usnea. In *U. longissima* he claims that the asci do not arise from the ascogonia, although several are present. Trichogynes and spermatia could not be found in *U. microcarpa*.

The presence of trichogynes, spermatia, and carpogonia similar to those of the red algae, and also ascogenous hyphae which arise from carpogonia, all indicate the presence of an undoubted functional sexual apparatus in the lichens, although the important phenomena relating to nuclear behavior still remain unsolved.

GUILLIERMOND (:**05**) has discovered a nuclear fusion accompanying cell fusion in certain yeasts which he holds to be sexual. Conjugation of conidia and nuclear fusion take place in the Schizosaccharomycetes and Zygosaccharomyces just before spore formation, while in certain other forms (*S. Ludwigii*, etc.) the same phenomena occur at the time of spore germination. In the Schizosaccharomycetes and Zygosaccharomyces two cells become connected by a conjugation tube in which nuclear fusion occurs. The fusion nucleus divides immediately and the two daughter nuclei separate, one entering each original cell, in which a double division occurs to form the four nuclei of the four so-called ascospores. In certain other yeasts, such as *S. Ludwigii*, projections are put out from contiguous spores in the ascus, fusing to form a canal in which nuclear fusion occurs. A promycelium is developed from this conjugation tube, which buds off conidia. GUILLIERMOND considers the phenomena here presented as the conjugation of isogamous gametes, in the one case before and in the other case after the formation of the asci. In the one case, *S. Ludwigii*, yeast of Johannisberg, and *S. saturnus*, the sporophyte with the double nuclear characters is the ordinary vegetative budding stage of the yeast, while in the other case (Schizosaccharomycetes and Zygosaccharomyces) this vegetative stage is the gametophyte.

The most recent investigations on the Ascomycetes and rusts indicate an undoubted alternation of generations in these groups. It will certainly be interesting, therefore, if the yeasts can be shown to exhibit like phenomena, but apparently these forms need to be further investigated before alternation of generations can be regarded as firmly established.

From the above résumé it will be seen that the doctrine of the sexuality of the Ascomycetes has steadily advanced since DEBARY's time, but an immense number of forms remain yet to be investigated as to the initial stages of the ascocarp. While much investigation has centered on the sexual apparatus, the study of the development of the ascospores has by no means been neglected. Within recent years a considerable literature has been developed relating to the cytology of the ascus. We are concerned more especially with the method of spore formation and the phenomena of chromosome reduction, and the literature of this phase of the subject may be summarized as follows:

GJURASIN ('93) first observed mitoses in the ascus of *Peziza vesiculosa*, maintaining that the divisions are karyokinetic and that the prophases and anaphases take place inside the nuclear membrane. He discovered well-marked asters but describes no centrosomes. In the last or third division the spindles are placed at right angles to the length of the ascus. The asters of these nuclei persist for a remarkably long time, and the astral rays, although not connected with the nuclei, are folded back over them.

DANGEARD ('94) in studying very young asci of *Peziza vesiculosa* and *Borrera ciliaris* discovered the two primary nuclei of the ascus, which fuse to form the large ascus nucleus. Four nuclei appear in the recurved tip of a young ascogenous hypha. By means of transverse walls the nuclei are so separated that one remains in the end cell, two in the penultimate cell, and one in the antepenultimate cell. The ascus grows out from the penultimate cell and the two nuclei fuse to form the ascus nucleus. This according to DANGEARD is a true sexual union.

HARPER ('95, '96, '97 '99, :00, :05) has made the most thorough study of the structure and division of the nuclei in a number of Ascomycetes. He discovered and described the rôle of the kinoplasmic fibers in the formation of spores. He first counted the number of chromosomes in several species. In *Pyronema confluens* he also observed that there are at first two nuclei in the recurved tip of an ascogenous hypha, which divide simultaneously by mitosis, thus forming four. One of each pair of nuclei enters the young ascus, which arises as an outgrowth of the penultimate cell. These two nuclei, which in this case are thus shown to be not sister nuclei, fuse to form the ascus nucleus. In a study of spore formation HARPER determined and fully described the process involved in the delimitation of the spores. Each nucleus forms a beak which is connected with a persistent central body, bearing at its outer end the astral rays. These rays bend backward and downward, finally coming in contact laterally and fusing to form a thin membrane, which continues to grow backward until a focal point is reached, thus completing the process of spore delimitation. This kinoplasmic membrane cuts the spore out of a homogeneous mass of protoplasm. He has described this process in *Erysiphe communis*, *Peziza vesiculosa*, *Ascobolus furfuraceus*, *Lachnea scutellata*, *Pyronema confluens*, and *Phyllactinia corylea.*

BERLESE ('99) has studied spore formation in *Tuber brumale*, concluding that the plasma membrane of the spore is formed from the astral rays. His results on nuclear phenomena agree essentially with those of GJURASIN and HARPER. MAIRE (:03, :04, :05) has described the nuclear divisions and ascus formation in *Galactinia succosa* and several other Ascomycetes, and confirms the method of spore formation as described by HARPER.

GUILLIERMOND (:03, :04, :05) studied several species with especial reference to karyokinetic division, the structure of the epiplasm, and the formation of the asci. He confirms the results of MAIRE on *Galactinia succosa*, finding that the tips of the ascogenous hyphae are not recurved, but that the terminal cells give rise to the asci. Wherever spore delimitation was studied it was found to follow the method described by HARPER.

BARKER (:03, :04) in a preliminary study of Ryparobius, a form whose asci contain more than eight spores, finds that the asci are formed from the penultimate cells of the ascogenous hyphae which contain two nuclei, these subsequently fusing to form the ascus nucleus. He also studied the nuclear divisions and spore formation. Sixty-four free nuclei are formed, which become regularly grouped in the peripheral, dense, granular protoplasm of the ascus. Other series of divisions usually occur and uninucleate spores are eventually formed. The details of spore formation have not been described by BARKER. The description of spore formation in this many-spored form will be of great value, and BARKER'S results will be awaited with interest. He is inclined to believe that the whole process of spore formation is intermediate between typical methods in sporangia and asci.

MAIRE (:05) concludes that in *Galactinia succosa*, *Pustularia vesiculosa*, *Rhytisma acerinum*, *Morchella esculenta*, *Anaptychia ciliaris*, and *Peltigera canina* the first division of the ascus nucleus is heterotypical, and that the second division is homeotypical. In the prophases of the first division he finds a well-marked synapsis stage. The asci are formed by two different processes, one of which is characterized by the formation of a hyphal system sympodially branched, each cell of which is a synkaryon containing two nuclei which divide by conjugate division. The binucleate terminal cells of these ascogenous hyphae become the asci. He believes that there is a tendency in the Ascomycetes to form a synkaryophyte analogous to that of the Basidiomycetes. MAIRE, however, has been unable to trace these synkaryons back to their first beginnings, which is highly important. In Galactinia the centrosomes and spindles have an intranuclear origin, while the polar asters have an extranuclear origin, developed independently of the intranuclear part. Nuclear beaks are formed in the process of spore delimitation.

GUILLIERMOND (:05) finds that in *Acetabula leucomelas* and in *Galactinia succosa* the ascogenous hyphae form a series of binucleate cells, the end cells of which become the asci. *Peziza catinus* presents still another method of ascus formation, which he holds to be analogous to that in *P. vesiculosa*. The terminal cells of the ascogenous hyphae are uninucleate, while the subterminal cells are binucleate. These binucleate subterminal cells bud out a lateral branch to form the ascus, which grows parallel to the filament, and in which nuclear fusion occurs to form the ascus nucleus. GUILLIERMOND has studied the behavior of the chromatin in the asci of *Pustularia vesiculosa*, *Peziza rutilans*, *P. catinus*, and *Galactinia succosa*, and believes that the first ascus mitosis is heterotypical, and that the first mitosis is preceded by a synapsis stage.

Faull (:05) in a cytological study particularly of *Hydnobolites* sp., *Neotiella albocincta*, and *Sordaria fimicola* finds also numerous cases in which the ascus does not arise from the penultimate cell of the recurved tip of the ascogenous hypha, as originally described by Dangeard. Such is invariably the case in only eleven out of the thirty-six species studied. In some species he claims that the asci bud out from the penultimate cells of the ascogenous hyphae, in others from the terminal cells, and in a few cases apparently from any cell. The uninucleate state of the ascus is preceded by a fusion of two nuclei, which may be sister nuclei. The centrosome and asters are extranuclear in origin, while the spindles are intranuclear. Enucleate portions of spores may be cut off, as in Podospora. Faull's description of spore formation is particularly interesting, as it differs entirely from that described by Harper. The spindle fibers elongate, bringing the daughter nuclei to the periphery of the sporeplasm, with their centrosomes in contact with the plasma membrane. The spores are delimited about each nucleus by the differentiation of a hyaline, finely granular protoplasm, which begins at the centrosome and finally entirely encloses the sporeplasm. The plasma membrane is subsequently formed from or in this hyaline area, and concurrently with this a second membrane is formed in contact with the first, lining the cavity in which the spore is to lie. Faull suggests that the membrane may arise by a cleavage in the limiting area, caused by its growth and differentiation, together with a pull on the part of the nucleus. Both plasma membranes are intimately concerned in laying down the exospore. He can find no evidence that the astral rays fuse to form a membrane which cuts out the sporeplasm. Faull also favors the view which homologizes the ascus with the zoosporangium of the Oomycetes, as an argument in favor of the origin of the Ascomycetes from the Oomycetes.

Faull (:06) also concludes that the ascus of the Laboulbeniaceae contains a fusion nucleus which divides by three successive divisions. The process of spore formation is, as he states, essentially the same as he has described for other Ascomycetes.

In *Humaria granulata* Blackman and Fraser (:06) find that the asci are usually developed from the subterminal cells of the recurved tips of the ascogenous hyphae. In two cases they found asci developed from the terminal cells of these hyphae, as described by Maire for *Galactinia succosa*. These authors have not made a detailed study of the nuclear phenomena, but believe that spore formation is essentially the same as described by Harper.

Ramlow (:**06**) finds that the single ascus of *Thelebolus stercoreus* arises directly from the ascogonium, as in Spaerotheca. The two primary ascus nuclei fuse, and the resulting nucleus by successive divisions forms an enormous number of free nuclei. The details of karyokinesis have not been followed, although he satisfied himself that the divisions are indirect. The nuclei are evenly distributed in the ascus. The phenomena of spore formation were not accurately determined, but Ramlow, basing his conclusions on the appearance of the protoplasm, which does not cleave as in the sporangium of the Phycomycetes, the appearance of an epiplasm, and the position of the nucleus at one end of the young spore, believes that the process of spore formation is by free cell formation, just as in Erysiphe.

The number of chromosomes recorded in Ascomycetes.

Plant	Chromosome number	Observer	Year
Aleuria cerea	8	Guilliermond	1903, 1904, 1905
Anaptychia ciliaris	4	Dangeard	1903
Anaptychia ciliaris	8	Maire	1904, 1905
Anaptychia ciliaris	8	Guilliermond	1905
Ascobolus furfuraceus	8	Harper	1895
Ascobolus furfuraceus	4	Dangeard	1903
Ascodesmis nigricans	4	Dangeard	1903
Endocarpon miniatum	4	Dangeard	1903
Erysiphe communis	8	Harper	1900
Galactinia succosa	4	Maire	1903, 1904, 1905
Galactinia succosa	8	Guilliermond	1905
Hydnobolites sp.	4 or 5	Faull	1905
Hypomyces Thiryanus	4	Maire	1905
Morchella esculenta	4	Dangeard	1903
Neotiella albocincta	6 or 7	Faull	1905
Otidea onotica	8	Guilliermond	1903, 1904
Peltigera canina	4	Maire	1904, 1905
Peziza catinus	12	Guilliermond	1903, 1904
Peziza catinus	16	Guilliermond	1905
Peziza rutilans	12	Guilliermond	1903
Peziza rutilans	16	Guilliermond	1904, 1905
Peziza Stevensoniana	8	Harper	1895
Phyllactinia corylea	8	Harper	1905
Pyronema confluens	10	Harper	1900
Pyronema confluens	4	Dangeard	1903
Pustularia vesiculosa	4	Maire	1904, 1905
Pustularia vesiculosa	8	Guilliermond	1905
Rhytisma acerinum	4	Maire	1904, 1905
Ryparobius sp.	8 (?)	Barker	1904
Sphaerotheca castagnei	4	Dangeard	1903

The determination of the number of chromosomes in the ascus as well as in other cells is of the highest importance, as it will indicate the real nature of alternation of generations in the higher fungi. Since the chromosome number has been determined by several authors for a number of species of Ascomycetes, it may prove useful to summarize the results. (See the foregoing table.)

That there is considerable difference of opinion as to the chromosome number even in the same species of some Ascomycetes is evident from the above table. In Ascobolus and Pyronema HARPER finds eight and ten respectively; while DANGEARD claims that there are four in both species. GUILLIERMOND and MAIRE have established the number eight for Anaptychia; while DANGEARD claims four for this species also. MAIRE counts four chromosomes in *Galactinia succosa* and *Pustularia vesiculosa*, while GUILLIERMOND claims that there are eight in each of these forms.

From the above résumé it seems perfectly evident that no such hypothesis as that the chromosome number four is general among the Ascomycetes, as DANGEARD imagines, can be maintained. In this group, on the contrary, judging from the above facts, related species may vary in their respective chromosome numbers, just as has been found to be the case in many of the higher plants.

In a recent paper MAIRE (:**05**) criticizes GUILLIERMOND (:**05**) for saying that he maintains that there are probably four chromosomes in all Ascomycetes, but admits that he and DANGEARD have formulated practically parallel hypotheses on this point. DANGEARD (:**03**), however, distinctly refers this hypothesis to MAIRE (Séance de la société mycologique de France tenue à Poitiers en Octobre, 1903), and says "Cette découverte a été faites simultanément et d'une manière indépendante par MAIRE et nous: elle offre, semble-t-il, toutes garanties de certitude." It appears from these facts that MAIRE has the responsibility of having first made the claim made by DANGEARD, but which MAIRE now attributes to him. It is perfectly plain that no basis for such a hypothesis exists, a fact which MAIRE apparently fully recognizes.

Since DANGEARD first described the asci in a number of forms as arising from the cell next the terminal one, several deviations from this type have been reported. That no such regular process of ascus formation obtains in general in the whole group of Ascomycetes, or even in nearly related genera, is clearly evident from a study of the more recent cytological investigations, especially those of MAIRE, GUILLIERMOND, and FAULL. In the following résumé no pretense of absolute completeness is made.

We may note first those very simple forms which have sometimes been classed together as Hemiasci, though in most cases, as KUYPER shows, the types are plainly not closely related. The genera Ascoidea (POPTA '99), Protomyces (SAPPIN-TROUFFY '97, POPTA '99), and Taphridium (JUEL :02) possess a septate mycelium with multinucleate cells, from which the sporangia arise directly without the intervention of sexual organs. The hyphal cells of Protascus (DANGEARD :03) also give rise directly to the asci. Sexual organs are present in Dipodascus (JUEL :02) and Eremascus (EIDAM '83), and the fertilized oogonium forms a single ascus. Monascus (BARKER :03, OLIVE :05) apparently forms a branched ascogenous hyphal system, each cell of which is able to produce an ascus. The heterogeneity of these forms is evident by the fact that the asci arise directly from an oogonium, from hyphal cells, or from the cells of ascogenous hyphae.

In some yeasts the conidia become transformed immediately after nuclear fusion into so-called asci, as in Schizosaccharomyces and Zygosaccharomyces, while in others the conidium is transformed directly into the ascus and fusion comes later, as in *S. Ludwigii* (GUILLIERMOND :05).

In the Exoasci the binucleate cells of the mycelium are transformed immediately into a single ascus, as in *Exoascus deformans* (DANGEARD '94) and Taphrina (SADEBECK '93, IKENO :01, :03). Among the Gymnoascaceae, *G. Reesii* and *G. candidus* (BARANETZKY '72, EIDAM '83, DALE :03) have their asci arising from the end cells of a series of short ascogenous hyphae. If CLAUSSEN'S (:05) Boudiera is really *Ascodesmis nigricans*, as CAVARA (:05) believes, and if Ascodesmis belongs among the Gymnoascaceae, then we have a form in this group whose asci arise from the penultimate cells of the recurved tips of the ascogenous hyphae.

The Perisporiaceae show considerable variation in the method of ascus formation. The early works of DEBARY and others may be passed over, as the methods used by them were not sufficiently delicate to enable them to determine the exact method of ascus formation. The end cells of ascogenous hyphae described by DEBARY for Eurotium, for example, may as well represent subterminal cells. In the mildew, *Erysiphe communis* (HARPER '96), the end cells of the ascogenous hyphae may develop the asci. This is also the case in *Phyllactinia corylea* (HARPER :05), but asci may also be formed as lateral branches of intercalary cells. In *Sphaerotheca castagnei* (HARPER '95) and *S. humuli* (BLACKMAN and FRASER :05) the oogonium develops into an ascogonium of five or six cells, of which the penultimate one grows into a single ascus. In this genus there are no ascogenous hyphae, unless we accept the interpretation of BLACKMAN and FRASER that the ascogonium is a single ascogenous hypha, whose penultimate cell develops an ascus in the manner described by DANGEARD. In *Anixia spadicea* (FAULL :05) the asci spring from any cell of the ascogenous hyphal system.

In the Tuberaceae, *T. melanospermum* (DANGEARD '94, GUILLIERMOND :04) has its asci arising as described by DANGEARD; while *Genea hispidula* (FAULL :05) shows a marked variation from this type. In this form the ascus grows out from a curved terminal cell. FAULL suggests that perhaps the only difference between this and the other type is the lack of a cross wall cutting off the uninucleate hyphal tip.

Among the apogamous Pyrenomycetes, such as *Teichospora trimorpha*, *T. aspera*, *T. nitida*, and *Teichosporella* sp. (Miss NICHOLS '96), a uninucleate ascus arises from a single central cell of the perithecial mass. *Hypomyces Thiryanus* (MAIRE :05) follows the method described by DANGEARD; while in *Podospora ascerina*, *P. setosa*, *Sordaria fimicola*, and *S. humana* (FAULL :05) the asci arise from a curved terminal cell of an ascogenous hypha. In *Phyllachora graminis* (FAULL :05) the ascus arises from a curved cell of the tip without the formation of a uninucleate tip-cell.

The Discomycetes are described as showing the greatest uniformity in the method of ascus formation, which may perhaps be due to the fact that more careful work has been done upon them. All the following forms have their asci formed in the manner described by DANGEARD ('94) for *Peziza vesiculosa*: *Borrera ciliaris*, *Acetabula* *calyx* (DANGEARD '94), *Peziza Stevensoniana, Ascobolus furfuraceus* (HARPER '95), *Lachnea scutellata, Pyronema confluens* (HARPER :00), *Aleuria cerea* (GUILLIERMOND :03, :04), *A. amplissima*, and *A. olivea* (GUILLIERMOND :04), *Peziza catinus, P. venosa, P. rutilans* (GUILLIERMOND :04), *Ascobolus marginatus, Otidea onotica* (GUILLIERMOND :03, :04), *Acetabula vulgaris, Pyronema confluens, Ciboria echinophila, Bulgaria inquinans, Guilliermondia saccabaloides* (GUILLIERMOND :04), *Peziza* sp. (FAULL :05), *Ryparobius* sp. (BARKER :03, :04), *Neotiella albocincta, Acetabula* sp., *Pseudoplectania* sp., (FAULL :05), *Boudiera Clausseni* (CLAUSSEN :05), *Peziza vesiculosa* (MAIRE :05), *Thelebolus stercoreus* (RAMLOW :06), *Humaria granulata* (BLACKMAN and FRASER :06), *Thecotheus Pelletieri* (OVERTON :06). Several variations from the type described above also occur among the Discomycetes. *Galactinia succosa* (MAIRE :03, :05, GUILLIERMOND: 03, :05), *Acetabula leucomelas* (GUILLIERMOND :03, :04, :05), *Acetabula vulgaris* (MAIRE :03) have their asci arising from binucleate terminal cells. GUILLIERMOND (:03) also found that *Pustularia vesiculosa* occasionally has its asci arising in a like manner. *Peziza catinus* and *P. vesiculosa* (GUILLIERMOND :05) occasionally have the asci arising from the subterminal cells of the ascogenous hyphae whose tips are recurved. *Acetabula acetabulum* (GUILLIERMOND :03) has binucleate cells formed in the curved tips of the ascogenous hyphae which do not form the asci, but give birth to a series of two, three, and four cells, of which the terminal ones produce the asci. In *Discina venosa* (FAULL :05) the ascus arises from a curved terminal cell. In *Urnula craterium* (FAULL :05) the ascus may spring apparently from any cell whatever. In *Humaria granulata* (BLACKMAN and FRASER :06) the ascus occasionally arises from the terminal cell.

A number of the Helvellaceae have been studied, which also show great variation in the mode of ascus formation. *Helvella ephippium* (DANGEARD '94), *Morchella esculenta* (DANGEARD '94), *Helvella sulcata, H. elastica, H. crispa* (GUILLIERMOND :04), *Morchella esculenta, M. conica, Helvella astra, H. lacunosa, H. elastica* (FAULL :05) have their asci formed from the penultimate cells of the recurved tips of the ascogenous hyphae, in the manner described by DANGEARD for Morchella. In *Geoglossum ophioglossoides, G. hir-*

sutum, *Geoglossum* sp., *Verpa conica*, *Gyromytra sphaerospora*, *Leptoglossum luteum*, *Leptoglossum* sp., *Mitrula phalloides*, *Leotia lubrica*, *L. chlorocephala* (FAULL :05) the ascus grows out from the terminal cell, and no uninucleate end cell is cut off. In *Verpa bohemica* (FAULL :05) is found the very greatest variability; the asci appearing as outgrowths of a terminal cell, or from a second, third, or even fourth cell from the tip.

The lichens *Anaptychia ciliaris* (DANGEARD :03), and *Peltigera canina* (MAIRE :05) have their asci regularly formed according to DANGEARD'S method; but *Anaptychia ciliaris* (MAIRE :05) apparently develops its asci from the subterminal cells of the ascogenous hyphae, while the tips, according to MAIRE, may continue development. BAUR (:01, :04), although he does not describe the method of ascus formation, figures ascogenous hyphae which are recurved in *Pertusaria communis*.

In the foregoing I have endeavored to group our knowledge of the various methods of ascus formation according to the natural classification of the forms investigated, in order that the significance of the variation described may be more apparent. It is the nuclear history which is theoretically most interesting, and is thus most essential to determine the relative ancestry of each of the nuclei which fuse in the ascus. This has been done for very few forms as yet. In Pyronema, HARPER (:00) has been able to trace the origin of the two primary nuclei of the ascus, in a case in which the tips of the ascogenous hyphae at first contain two nuclei. These divide by simultaneous division. Of the four nuclei thus formed, one lies in the terminal cell, and two, which are not sister nuclei, in the subterminal cell which becomes the ascus.

Thecotheus belongs to that group of the Discomycetes (Ascobolaceae) whose small fruit bodies are nearly always found growing freely on dung. The species in question occurs on horse dung. It was found on cultures which were old and partly dried up in the Botanical Laboratory of the University of Wisconsin. These cultures were kept running, yielding an abundant supply of material during the progress of this investigation. The fungus has since been found free in nature. The apothecia are very small, about 0.5^{mm} in diameter and 0.25^{mm} high, of a white or yellowish color. When wet they are therefore plainly visible to the naked eye. A distinct thin excipulum, or lateral boundary of vegetative hyphae, surrounds the hymenium (*fig. 3*). This excipulum is densely covered with short, blunt ends of protruding vegetative hyphae, which give a hairy or warty appearance to its surface. The sterile tissue of the secondary mycelium extends outward and downward to form a pseudo-parenchymatous skirt-like structure, which also extends along the substratum beneath the hypothecium. This lower layer becomes adjusted to the irregularities of the substratum, from which numerous hyphae enter the fructification. The equilibrium of the whole fruit body is maintained by means of this much broadened pseudo-parenchymatous base (*fig. 3*).

The apothecia are at first globular or cylindrical, later becoming broadened, discoid, and somewhat biscuit-shaped (*fig. 2*). The asci are roughly cylindrical in form, about $220 \times 35\mu$, their greatest diameter being near the top. Each ascus contains thirty-two ellipsoidal, slightly colored spores, each about $17.5 \times 28\mu$, which are discharged through a small terminal pore. This pore is at first covered by a small cap or operculum, bounded by a thickened ring in the wall of the ascus where the cover breaks off (*fig. 16*). The asci develop from the subhymenium successively; each fruit body thus contains asci and spores in all stages of development. Numerous long and slender septate paraphyses, about 360μ long, arising from the hypothecium, are thickly packed among the asci. At the surface each paraphysis has a somewhat swollen protruding tip (*figs. 2, 3*). The mature spore contains a single nucleus in a mass of very densely granular protoplasm (*fig. 15*). The thin, very pale exospore is corrugated on its outer surface, much like many other spores of the Ascobolaceae. There is a passage through this exospore at each end, as well as through the thick hyaline endospore, to form what is apparently a terminal germinal pore. The spores are not shot out of the asci, but appear to be squeezed out by turgor, together with the lateral pressure exerted by the turgor of the neighboring asci and paraphyses. They are to be found as a dust on the surface of the apothecium, often adhering in masses. Possibly in consequence of the smallness of the terminal aperture of the ascus the spores are not projected or discharged violently. This condition is not general among other forms of the Ascobolaceae, in most of which the spores are projected for some distance through the terminal pore of the ascus.

Modifications of the usual strengths of Flemming's chromacetic osmium fixing fluids were exclusively used in the preparation of the material. Portions of the substratum upon which apothecia grew were removed and dropped into the fluids. Beside the mature fruits many younger stages were thus obtained. The sections were stained with safranin gentian-violet orange-G combinations and also with Heidenhain's iron-alum haematoxylin. The sections were cut 5–10 μ thick.

Harper ('95, '96, :05) has shown that the ascogonia of the mildews consists of a much curved row of cells, each of which contains a single nucleus, with the exception of the penultimate cell, which contains two or several nuclei, and which forms the ascus in Sphaerotheca, out of which grow the ascogenous hyphae in other forms. Barker (:03, :04) also observed the same kind of ascogonium in Ryparobius; while Claussen (:05) finds several such ascogonia in Boudiera. The youngest ascogonium which I have thus far observed in Thecotheus consisted of a row of several cells which were already multinucleate (*fig. 1*). Harper ('96) figures and describes perforations in the cross walls in the ascogonium of Ascobolus connecting the adjacent cells. One of the cells of the row is larger. It is from this particular cell that the ascogenous hyphae arise, and out of which the nuclei enter the ascogenous hyphae from it and the neighboring cells. As soon as the ascogonia become empty they undergo disintegration. Barker (:04) finds each cell of the row in Ryparobius at first uninucleate and then binucleate or occasionally quadrinucleate. From the cells of the row the ascogenous hyphae delevop. He does not distinctly say that they develop from any particular cell of the ascogonium. Claussen (:05) finds that the gametes of Boudiera contain several nuclei, which however fuse in pairs in the oogonium. Several walls are formed, so that the resulting ascogonium consists of a row of several cells from which the ascogenous hyphae arise. Thecotheus agrees with Ryparobius and Boudiera in that the ascogenous hyphae do not arise from any single cell of the ascogonium, but from any or all of them (*figs. 1* and *2*). The youngest ascogonia which I have been able to find were already multinucleate, some containing as many as a dozen nuclei, each much larger than those of the vegetative cells. *Fig. 1* shows a young fruit body with sections of several ascogonia, each of whose cells are multinucleate. No connections between the adjacent cells could be observed.

Unlike Ryparobius and like Boudiera, Thecotheus has a compound fruit body. *Fig. 1* represents a section of a young ascocarp, in which several ascogonia are present. One ascogonium, composed of several multinucleate cells, is shown, which resembles in shape the ascogonium of Ascobolus. In the same section, surrounded by the same investment of vegetative hyphae, may be seen also sections of several other ascogonia. These ascogonia are always closely interwoven, so that they are cut in different planes. Other views of the same ascogonia appear in adjacent sections of this ascocarp.

Concurrently with the development of ascogenous hyphae, investing vegetative hyphae encircle the ascogonia, the young ascogenous hyphae, and the asci. This condition can be seen in *fig. 2*. Remnants of the ascogonia are still plainly visible, and the branching ascogenous hyphae can be seen to contain several nuclei, each with a single nucleolus. The nuclei of the ascogenous hyphae are from three to four times as large as those of the paraphyses, making them therefore easily distinguishable. Each cell of the vegetative tissue contains several nuclei. I have been unable to find any regular series of binucleate cells.

The developing ascogenous hyphae are profusely branched, pursuing such irregular paths that it is impossible to follow their course for any great distance. Transverse longitudinal and oblique sections appear in the preparations, which are only mere fragments of the whole system (*fig. 2*). From *fig. 2*, however, it is plain that the ascogenous hyphae develop considerably before transverse septa are put in. The nuclei are especially abundant near the tips of the branches. At the time the cell division is complete, the tips of the branches of the ascogenous hyphae are bent backward as they push upward among other branches and paraphyses. The terminal cell is uninucleate, while the subterminal cell is binucleate. The nuclei of these branches can be seen to be considerably larger than those of the ascogonium (*fig. 4*). From these binucleate subterminal cells the asci develop. So far as I have been able to observe, asci were never developed from the terminal cell, or from the third cell from the tip, although either condition may possibly occur. Thecotheus certainly does not contain a system of ascogenous hyphae, each cell of which is a synkaryon, as described for Galactinia and *Pustularia vesiculosa*.

In Thecotheus the subterminal cell of an ascogenous hypha arches up to form the young ascus. The two nuclei apparently fuse to form the ascus nucleus (*fig. 4*). The young club-shaped ascus is filled with a dense finely granular vacuolated protoplasm, in which are situated numerous deeply staining extranuclear granules, probably the metachromatic granules of GUILLIERMOND (:**03**), which have also been observed and described by other authors. The fusion nucleus greatly enlarges as the ascus grows, thus maintaining a definite nucleo-cytoplasmic relationship, as described by HARPER (:**05**). Within the nucleus chromatic filaments are organized, which give the appearance of a loose spirem. Division stages were not observed, but, so far as I have been able to find, the nuclear structures are essentially the same as have already been many times described.

The young ascus, which elongates rapidly, crowding up into the hymenium, is somewhat broadened at its tip, gradually narrowing toward the base. The protoplasm, packed in the tip, is coarse and granular (*fig. 7*). A spore region is organized about the nucleus. A large region, in which the protoplasm is very foamy, is present both above and below the central denser sporeplasm. The ascus increases still more in size, the denser regions at the apex and about the nucleus becoming still more sharply separated by the large vacuolated space (*fig. 8*). A peripheral layer of denser protoplasm connects the apical and central regions. The distinction of central and apical regions and the two large vacuolated spaces with foamy protoplasm persist throughout the process of spore formation (*figs. 8–12*). The primary ascus nucleus divides rapidly by three successive divisions to form eight free nuclei. During these divisions there is a gradual decrease in the size of the nuclei, as has also been observed in other asci. In *fig. 10* it will be seen that each of the eight nuclei are very small compared with the nuclei represented in *figs. 7* and *8*. From the abundant stages found in the conditions represented in *fig. 10*, I am inclined to believe that there is a pause before further divisions occur and a growth period of these eight nuclei. Not only do the nuclei increase in size before dividing, but the asci also lengthen very much and the protoplasm becomes still more vacuolated and foamy (*fig. 11*). Perhaps this increase in size of the nuclei is also correlated with the increase in the amount of cytoplasm in the ascus. Eventually each of these eight nuclei divides to give sixteen free nuclei, no spores being yet delimited (*fig. 11*). In *fig. 11* each nucleus is about as large as one of the daughter nuclei in *fig. 8.* These nuclei certainly show a marked increase in size over those of *fig. 10.* It will also be observed that the nuclei are irregularly arranged in the central region of the sporeplasm. Each of these sixteen nuclei undergoes still another division, resulting in thirty-two free nuclei being found in the ascus. No figure representing this thirty-two nucleate stage has been drawn, although the nuclei were seen in the preparations. *Fig. 6* represents a portion of such a stage. The nuclei here are also very much smaller than in *fig. 11.*

In Ryparobius BARKER (:**03**, :**04**) finds that the number and size of the spores vary in different asci. More than two hundred were normally found in a single ascus, but as few as sixteen have been seen. In Ryparobius successive nuclear divisions occur rapidly, until sixty-four free nuclei are formed. These become regularly grouped in a dense granular mass of protoplasm around the periphery of the ascus. Other series of divisions now usually occur, and eventually uninucleate spores are formed. In Thelebolus (RAMLOW :**06**) many nuclei arise in the ascus, about each of which a spore is delimited, as described by HARPER.

In Thecotheus the spores are delimited from the homogeneous central portion of the cytoplasm immediately after the formation of the thirty-two nuclei. So far as I have been able to observe, the entire process of spore delimitation is accomplished by means of the kinoplasmic fibers which form the astral radiations of the central body. The nucleus becomes pointed or beaked, bearing a central body at its outer end, from which the kinoplasmic radiations extend (*fig. 6*). The chromatin lies freely in the nuclear cavity, apparently connected with the central body. The process of spore delimitation is apparently precisely like that described by HARPER for *Erysiphe communis*, *Lachnea scutellata*, *Pyronema confluens*, and *Phyllactinia corylea*. As soon as the beak has reached a certain length, which is comparatively short in Thecotheus, these kinoplasmic fibers bend downward and grow backward over the nucleus, fusing laterally to form a continuous plasma membrane, which separates the cytoplasm of the spore from that of the epiplasm. The nuclear beak is withdrawn and a somewhat pointed nucleus remains in the young spore (*fig. 6*), which gradually resumes the spherical shape of a resting nucleus. Although the process of spore delimitation is not easily followed in Thecotheus, I am convinced that it is essentially the same as HARPER has described for other Ascomycetes. I have also had an opportunity to compare my own preparations containing this stage with those of HARPER on Erysiphe and Lachnea, which objects he found most favorable for study. I can see no essential differences in appearances. The nuclear beaks do not have any special orientation or relation to the plasma membrane, as has been figured and described by certain authors for other forms. The beaks may lie at any angle during the process of spore delimitation.

BARKER (:**04**) believes the process of spore formation in the many-spored asci of Ryparobius to be unlike that in the typical ascus. "The protoplasm passes through a series of characteristic changes during the development of the ascus, and the whole process of spore formation seems to be intermediate between typical methods in sporangia and asci." We shall await BARKER'S completed account of the spore formation in this form with great interest. We have seen that the method of spore delimitation in the many-spored asci of Thecotheus is exactly similar to that found in typical eight-spored asci. As noted in another connection, FAULL entirely dissents from the method of spore formation as described by HARPER. I have been unable to discover in Thecotheus the presence of hyaline zones in connection with which cleavage takes place to delimit the sporeplasm from the epiplasm as described by FAULL, and I am certain that no such method of spore formation exists in Thecotheus.

Fig. 6 represents a spore in the process of delimitation as described above. In the same figure a very young spore is also shown, which has its delimiting membrane already formed and the nuclear beak withdrawn. It will be observed that the sporeplasm is nearly like the surrounding epiplasm, perhaps slightly more dense and granular. No particular granular area is present. It is simply a portion carved out of the homogeneous cytoplasm in which the nucleus is situated by means of a delimiting kinoplasmic membrane. In *figs. 12a–12c* slightly older spores are shown. They are arranged in the form of a hollow cylinder around the wall of the ascus. About five young spores are arranged vertically along the ascus walls in any one plane. *Fig. 12a* represents a median longitudinal section of the ascus; *figs. 12a* and *12b* are slices off the same ascus.

BARKER (:03) found that the numerous nuclei in the asci of Ryparobius became arranged in the form of a hollow sphere just beneath the wall of the ascus before spore delimitation. Each ascospore when completely formed, therefore, has one end toward the center and the other toward the ascus wall, the resulting arrangement of the spores thus being radial. In Thecotheus the nuclei, as noted above, are not arranged radially, but in the form of a hollow cylinder about the wall of the ascus, in a denser peripheral layer of the epiplasm. The resulting spores, therefore, have their long axes parallel to the wall of the ascus. In this respect Ryparobius and Thecotheus are essentially different. Due to this peripheral arrangement into a hollow cylinder, the spores are forced to occupy considerable space in the ascus, some being pushed up near the tip. The epiplasm is at this time everywhere much more vacuolated than in earlier stages, and the ascus is exceedingly turgid and swollen (*figs. 12a–12c.*)

In *fig. 12a* the spores can be seen to show no sign of an exospore or endospore. DEBARY ('63, '64) thought that the exospore was laid down upon the surface of the spore from the epiplasm, which explanation seems to have gained rather widespread acceptance. The exact method of exospore formation needs investigation. FAULL (:05) believes that two membranes are formed, one being the plasma-membrane of the spore and another formed concurrently with this, which lines the cavity in which the spore is to lie. These membranes occupy the position of the hyaline zone described above. The spore wall is supposed to be laid down between the membrane bounding the epiplasm and the plasma membrane of the spore. FAULL suggests that both membranes are perhaps active in the formation of the spore coats.

According to my own observations, the process of the formation of the spore coats does not agree with the account of FAULL (:**05**) *Fig. 13* shows a young spore which has grown somewhat beyond those found in *figs. 12a–12c*. The limiting membrane is not perceptibly thickened, showing in sections as an even unbroken line. Just inside this membrane, however, the endospore is seen to be but slightly differentiated from the sporeplasm, being much less vacuolated but more hyaline and granular. A more or less distinct boundary is present between the endospore and the sporeplasm. Exactly how the endospore is formed I am at present unable to state, unless it is laid down by the original plasma membrane, which has gradually withdrawn, secreting the substance of the spore coats as it recedes. Finally, the endospore becomes still more granular and hyaline as the spore develops (*fig. 14*). The outermost portion of the hyaline granular area constitutes the exospore. In *fig. 14*, which is not so highly magnified as *fig. 13*, the central portion of the sporeplasm is highly vacuolated. The nucleus of the spore lies in the center of this mass of protoplasm. The irregularities on the exospore may be due to fixation. Lines are developed on the surface of the spore, finally producing an irregularly branched system of elevations and ridges much like that found on the spores Ascobolus. *Fig. 15* represents a mature spore. The two germinal pores, one at either end, are present, passing through the spore coats. The mature endospore is very granular and highly refractive. The inner protoplasm, bounded by the plasma membrane, is still uninucleate but densely granular. Smaller vacuoles have entirely disappeared. In some mature spores two large spherical oil drops are present, one at either side of the nucleus, but not regularly so. *Fig. 15* is typical.

As the asci dry out, the walls become thickened and hyaline. *Fig. 16* shows the upper portion of a nearly mature ascus, at the apex of which is the cap or operculum in the process of formation. A thickened ring in the ascus wall is formed below the operculum. The mature spores are probably discharged through this terminal pore by the turgor of the ascus and the lateral pressure of other asci and paraphyses. Although several attempts were made to germinate these spores in various sorts of media, I have thus far been unsuccessful. Perhaps it may be necessary for them to pass through an alimentary tract or to be naturally or artificially partly digested before germination will occur, or perhaps the spores tested may not have been mature.

I have shown that ascogonia are present from which the asci arise, although I have been unable to find the earliest stages of these organs in Thecotheus. Since in the forms in which sexual organs do exist, as described by several investigators, an ascogonium arises as the result of nuclear and cell divisions from a fertilized oogonium, I think it practically certain that such oogonia exist in Thecotheus. Since the ascogonia are in groups, several being present in each young ascocarp, it is also safe to conclude that the fruit bodies arise as the product of multiple sex organs, just as in Pyronema and Boudiera. Thecotheus, therefore, is another example of a form among the Ascobolaceae with a compound apothecium.

In Thecotheus the asci are developed from the penultimate cells of the recurved tips of the ascogenous hyphae, and they are at first binucleate, later becoming uninucleate in the usual manner. There is apparently no tendency here toward the condition described by MAIRE and GUILLIERMOND, wherein a system of binucleate cells are formed, as in Galactinia, corresponding to the synkaryophyte in which a long series of binucleate cells occur, the nuclei finally fusing in the basidium, as in the Basidiomycetes and rusts. MAIRE claims to have found that these binucleate cells of the ascogenous hyphae originate from hyphae of the subhymenium, whose cells are multinucleate. The first cell arising from these subhymenial hyphae contains two nuclei, which divide by a conjugate division, giving rise to a series of branching synkaryophytic hyphae, which eventually form the asci. This branched, ascogenous hyphal system MAIRE compares to the hyphal system which gives rise to the basidia in the Basidiomycetes. Although MAIRE and GUILLIERMOND have found this system of ascogenous hyphae in certain forms, it still remains and is of the highest importance to determine how the ascocarps originate in these forms. If, as HARPER (:**05**) suggests, the condition found in Pyronema, and still more advanced in Galactinia and *Pustularia vesiculosa*, could work back until the egg cell was reached, an apogamous condition might result, such as is now found in the Hymenomycetes (Miss NICHOLS :**04**), and the nuclear fusion in the ascus might have acquired secondarily a sexual significance. Thecotheus with its ascogonia, and presumably also still earlier oogonia, shows no tendency towards this condition. I have been unable to find binucleate cells either in the paraphyses, in the mycelium, or in any of the vegetative cells of this fungus, and am sure that Thecotheus does not possess anything comparable to the synkarophyte of the Basidiomycetes.

The main problem relating to the asci at present is whether they are merely eight-spored sporangia or spore mother cells corresponding to those of the higher plants, and on this point the method of spore formation in a polysporous ascus should throw much light. As noted previously, I have confined my attention principally to Thecotheus on account of the abundance of this apparently very favorable form. The possibility that such asci might show transitional conditions leading over to those found in the sporangia of the lower fungi is very suggestive, and, as noted above, BARKER believes that in the asci of the nearly related genus Ryparobius he has found such transitional forms, although RAMLOW believes the ascus of Thelebolus shows no such sporangial characters. The distinction between typical sporangia and typical asci seems to be sharply drawn. In the sporangia of Sporodinia and Pilobolus HARPER ('99) has found that spore formation is by a process of progressive cleavage by means of furrows, either from the surface of the protoplasm or from vacuoles of the mother cell. The nuclei during the cleavage are in a resting stage and are not concerned in the process. Thus the formation of an epiplasm is precluded. HARPER has described the process of cell formation in *Synchitrium decipiens*, *Pilobolus crystallinus*, and *Sporodinia grandis;* while SWINGLE (:03) has observed the same process in the sporangia of *Rhizopus nigricans* and *Phycomyces nitens*. HARPER has pointed out that this process is not one of free cell formation in the sense in which the term is used for free cell formation in the ascus, in which the cells lie free in the mother cell included in the so-called epiplasm. He also concludes that these two very divergent methods of cell formation in asci and sporangia make it impossible to assume any close relationship between these two structures, and this difference is thus made an argument against the homology of the sporangium of the Phycomycetes and the ascus of the Ascomycetes.

Although attempts have recently been made to discredit HARPER'S results on the method of free cell formation in the ascus, no very convincing evidence has been brought forward to show that it is more like that in the sporangium. JUEL (:**02**) in his work on Taphridium seems to think that HARPER has placed too much stress on the action of the kinoplasmic fibers as one of the chief distinguishing characteristics of the process, saying: "Vorläüfig können wir nicht die Rolle des Kinoplasmas bei der Zellbildung zur *nota characteristica* der freien Zellbildung machen, sondern müssen diesen Begriff in der herrkömmlichen Weise auffassen." Apparently JUEL has failed to comprehend the essence of HARPER'S definition.

FAULL (:**05**) does not believe that the methods of spore formation in the ascus and sporangium are so different as to prevent assumption of their homology. He favors the view that homologizes the ascus with the zoosporangium of the Oomycetes, as an argument in favor of the origin of the Ascomycetes from the Oomycetes. The most complete account of cell formation in the zoosporangia of the Oomycetes is that given for Saprolegnia and Achlya, although the behavior of the nuclei has not been thoroughly enough studied.

The earliest workers in the study of spore formation were influenced by their *a priori* views on the cell theory as a whole, and NÄGELI used it to support his doctrine that new cells are regularly formed by so-called free cell formation from old ones. PRINGSHEIM ('**51**) believed that spores were formed by simultaneous and not by successive bipartitions of the protoplasm, being completely bounded off before the appearance of a cellulose wall. BÜSGEN ('**82**) in his description of spore formation in the sporangium of the Phycomycetes believed that cleavage is due to a simultaneous formation of cell plates, which break down, being later formed again to separate the spores. BERTHOLD ('**86**) studied oogonia, but assumed that the process in oogonia and sporangia are alike. The peripheral layer of protoplasm which surrounds the central vacuole forms dense rounded masses about definite centers, which constantly increase in size, protruding gradually into the central vacuole. Finally the masses separate and round up, later swelling up so as to become pressed together and flattened. Finally these masses again round up, forming definite eggs or swarm spores. BERTHOLD claims that the position of the spores is predetermined by centers of attraction, about which the protoplasmic lining of the walls is collected. The whole process is a form of free cell formation, in which the entire protoplasm is utilized, without involving the formation of a periplasm. He holds, therefore, that the sporangium of the Saprolegniaceae represents an advance over forms in which periplasm is formed. The sporangium is differentiated into central vacuole and peripheral protoplasm, and is perhaps a stratified structure in itself, whose polarity is determined by the position of the nuclei, which in turn influence the position of the spores, as has been pointed out by HARPER ('99).

According to the work of ROTHERT ('88), HARTOG ('88), HUMPHREY ('92), TROW ('95), and DAVIS (:03), the sporangium is multinucleate when cut off, the nuclei lying scattered in the peripheral layer of protoplasm. DAVIS practically confirms the account of the earlier authors. The uninucleate spores originate by means of clefts, which proceed from the central vacuole of the sporangium to the periphery, dividing the protoplasm into polygonal areas. The spores are later formed from these uninucleate areas. There is no mitotic division of the nuclei or cytoplasmic centers (coenocentra) in the zoosporangia.

HUMPHREY ('92) first studied oogenesis in Saprolegnia by means of modern technique, but was soon followed by TROW ('95, '99) and HARTOG ('95, '96, '99). There seems to be a great diversity of opinion as to the behavior of the nuclei, which far exceed the ultimate number used in the formation of eggs. HUMPHREY and HARTOG believe that the nuclei fuse in groups to form the functional nuclei. TROW claims that many nuclei degenerate until the requisite number is reached, which results DAVIS (:03) has confirmed, but differs from TROW in regard to the sexuality of the Saprolegniaceae. The oogonium arises as an enlargement of the end of a hypha, into which passes a dense mass of cytoplasm and nuclei. A central vacuole is formed, with a peripheral layer of protoplasm lining the walls in which lie the nuclei. The nuclei divide once by mitosis. The protoplasm aggregates into masses which form the eggs. The process of separating these masses by means of a series of fusing vacuoles, has been described by DAVIS. He finds that the egg initials are formed about cytoplasmic centers (coenocentra), much as has been described for certain Peronosporaceae. It seems apparent that, even if we accept FAULL's description of spore formation in the ascus, the data are quite insufficient to support any view which homologizes the ascus with the zoosporangium or oosporangium of the Oomycetes.

BARKER (:**04**) announces that the protoplasm in the developing ascus of Ryparobius shows a series of changes in spore formation, which appear to be intermediate between typical methods in sporangia and asci. The account is only preliminary and has been referred to above. My own studies on the asci of Thecotheus however, have shown the process of spore formation to be as in other typical asci, namely, by means of the kinoplasmic radiations of the nucleus. Although more than eight spores are formed in the ascus, the process of spore delimitation is that found in a typical ascus. There is absolutely no evidence that the process is in the least similar to spore formation as found in the sporangia of the Oomycetes or in those of the Phycomycetes. The results obtained do not seem to throw the least light on the homology or origin of this peculiar organ. It apparently makes no difference whether less than eight spores are formed or more than eight, the phenomena of spore delimitation are exactly the same as found in typical eight-spored asci.

That a true alternation of generations, comparable to that found in the higher plants, exists among the Ascomycetes, is certainly obvious from the fact that the asci eventually arise as the result of fertilization. DEBARY ('**70**) advanced the opinion that the ascus fruit represents an asexual generation, and WORONIN ('**70**) compared it to the sporogonium of the moss, which idea was farther emphasized by HARPER ('**96**) for Erysiphe. The only essential difference is that the egg is never separated from the parental tissue system, agreeing in this respect with that of the red algae. HARPER also pointed out that the ascus is an analogue of the spore mother cell of the higher plants, and that the triple division corresponds to the double division in the spore mother cells of the higher plants, with a probable consequent chromosome reduction in the ascus. This view is further supported by the recent discoveries of MAIRE (:**05**), HARPER (:**05**), and GUILLIERMOND (:**05**) on the nuclear phenomena in the ascus, by which reduction of the number of chromosomes and a consequent return to the gametophyte generally occur. These authors have found that the first division of the ascus nucleus is preceded by a well-marked synapsis phase, which the most recent zoological and botanical investigations have shown to be the most characteristic and important phase of the heterotypical division. While MAIRE finds a synapsis similar to that described by STRASBURGER (:04), HARPER and GUILLIERMOND have found the phenomena to be essentially the same as in the pollen mother cells of the flowering plants studied by GRÉGOIRE (:04), BERGHS (:04, :05), ALLEN (:04, :05), ROSENBERG (:05), STRASBURGER (:05), MIYAKI (:05), OVERTON (:05), TISCHLER, (:06), and CARDIFF (:06). HARPER finds permanent central bodies in the nuclei of Phyllactinia, and that the chromosomes are permanently attached to the central body and are thus brought side by side in nuclear fusion. On this ground he concludes that the chromosomes are permanent structures, and that they must be bivalent in the nuclei of the young ascus, due to the earlier fusion of the sexual nuclei. These bivalent chromosomes, he holds, further unite in synapsis to form quadrivalent structures, consisting of four somatic chromosomes arranged side by side, thus accounting for a numerical reduction just as in the higher plants. MAIRE says that the first division of the ascus nucleus is heterotypical, while the second is homeotypical, which opinion GUILLIERMOND also holds. HARPER gives no opinion as to which are the reduction divisions. He has pointed out, however, the universality of the occurrence of the double division, following synapsis in the spore mother cells of all higher plants, as necessary to accomplish chromosome reduction, where the chromosomes are bivalent structures. I might also call attention in this connection to the elimination of the double division in embryo sac mother cells of parthenogenetic angiosperms, discovered by JUEL (:00, :05), MURBECK (:01), OVERTON (:04), and STRASBURGER (:05), where reduction is not completed.

HARPER also points out that the universal triple division occurring in the ascus, no matter how many spores are to be formed, is probably to be associated with a quadrivalent character of the chromosomes in the ascus nucleus. Where one nuclear fusion occurs, as in most plants and animals, a double division is necessary to complete the reduction and to distribute the elements to the daughter nuclei; while when two nuclear fusions occur, as in Ascomycetes, a triple division and a double reduction is necessary to accomplish the same results. This triple division of the ascus nucleus occurs universally, whether two spores, four spores, or eight spores are to be formed. HARPER has pointed out how fundamental this triple division is, since when only two spores are to be formed, as in Phyllactinia, six nuclei degenerate. In such cases the three divisions constitute a single continuous process. That all these divisions persist, no matter how many spores are to be produced, shows their necessity in the process of reduction.

The work of BLACKMAN (:**04**) and his students (:**06**) and of CHRISTMAN (:**05**) have established an undoubted alternation of generations in the rusts, showing that in these forms the series of binucleate cells originate as a result of fertilization. The gamete nuclei persist throughout the sporophyte generation as independent nuclei, dividing by a conjugate division. In the teleutospore these nuclei fuse, and a synapsis stage occurs, followed by a double division which leads to the formation of the four nuclei of the four sporidia. As HARPER suggests, there is a striking parallelism between the teleutospore and the spore mother cell of the higher plants. He believes we are justified in regarding the first and second divisions in the promycelium as respectively heterotypical and homeotypical. As there is only one nuclear fusion in the life cycle of the rust, a consequent double division occurs in reduction. MAIRE (:**05**), finding in Galactinia that certain of the cells of the ascogenous hyphae which give rise to the asci are binucleate, holds to the conception that these binucleate cells correspond to those of the Basidiomycetes as well as to those of the rusts. There should be a series of binucleate cells in the sporophyte in all these groups, whose nuclei should divide by conjugate division, fusion first taking place in the basidium, in the teleutospore, and in the ascus, each of which would be comparable to the spore mother cells of the higher plants. This explanation does not explain, however, the universal occurrence of the third division, which is so general among the Ascomycetes, and which FAULL has found to occur in the Laboulbeniaceae; nor does it account for the apparently secondary nature of the fusions described by BLACKMAN and CHRISTMAN, as compared to those of the red algae, lichens, mildews, and Pyronema. It is certainly of great importance to know how the ascocarps of Galactinia, Acetabulum, and Pustularia arise, and whether apogamy or parthenogenesis is associated with the appearance of binucleate cells in the ascogenous hyphae.

The cells of the ascogenous hyphae of Thecotheus are not binucleate, and I am inclined to accept for this form HARPER's interpretation that the asci are spore mother cells, modified by adaptation as explosive organs and as reservoirs of reserve food supply, in which a merely vegetative fusion has occurred to maintain a definite nucleo-cytoplasmic relationship. A triple division follows to complete the reduction and distribution of the somatic chromosomes to each of the resulting eight nuclei. The sporophyte would thus include the ascogenous hyphae and the asci up to the time of the reduction division, which initiates the gametophyte generation.

In the typical ascus the nuclei of the eight spores contain the gametophyte number of chromosomes, as would also be true when only two or four spores are formed. When any of these spores germinate, they give rise to true gametophyte structures, usually a septate mycelium, which may reproduce itself asexually by conidia before sexual reproduction, as in Eurotium or Erysiphe. It is well known that many ascospores contain more than one nucleus, and, as FAULL and others have shown, these nuclei are formed by mitotic division of the primary spore nucleus. The spore may be septate or non-septate. The typical ascospore is uninucleate and non-septate. Both the number of nuclei and the number of septa in a spore vary from one to many. Spores which are septate have apparently begun an intrasporal germination, the gametophyte forming considerable embryonic tissue within the old spore wall. Spores which are not septate but multinucleate have also undergone embryonic development, but without cell division.

We perhaps should expect from what we know of other Ascomycetes that in many-spored asci, as in Thecotheus and Ryparobius, spores would be delimited as soon as eight free nuclei were formed. This does not occur in either of these forms, but further nuclear divisions take place before the spores are delimited. A closer analysis, however, shows that we have analogies for these conditions in the behavior of other undoubted spore mother cells. Intrasporal germination may be looked upon as comparable to that which occurs in the spores of many of the pteridophytes and spermatophytes. The spore not only begins its germination while inside the sporangium, but while it is still inside the mother cell. The ascus is not only to be looked upon as a mother cell, but also as a mother cell which functions directly as a sporangium. The prevalent impression is that the history of the gametophyte begins with the division of the mother cell and ends in the act of fertilization. The ordinary product of the division of the spore mother cell is four spores, or in typical Ascomycetes eight spores. In Lilium the first mitosis of the mother cell is heterotypical, while the second corresponds exactly in all details to the second division where normal tetrads are to be formed. We have here a double division completed inside the mother cell, and consequent germination to form a gametophyte inside the mother cell. It does not seem inconsistent, therefore, to think of a mother cell containing a gametophyte, or that the reduction divisions may not give rise directly to morphological spores. These nuclei are gametophytic in character and can give rise to gametophyte structures in the embryo sac. It is not absolutely essential, therefore, that the double division result in spore formation. JUEL (:**00**) found that in *Carex acuta* the usual double division occurs in pollen mother cells, complete cell plates being formed which are later resorbed, so that four nuclei lie inside the wall of the mother cell, three of which disintegrate, the fourth forming a single functional microspore. In Fuchsia (WILLE '**86**) as many as fourteen microspores have been reported from a single mother cell, while more or less than four have been found in several other forms. STRASBURGER and JUEL have also counted numerous microspores formed from a single mother cell. It would appear, therefore, that the double division is necessary, but that the number of spores ultimately formed is very variable. If in Fuchsia the walls of the microspores were eliminated, a striking resemblance to the sixteen-nucleate stage of Thecotheus would result. The number of spores formed and the time of their formation seems to be very variable, but this does not interfere with our conception of the alternation of generations in the flowering plants. That thirty-two free nuclei are formed in Thecotheus before spore delimitation occurs is therefore no more striking than that tetrads are not formed as a result of the double division in Lilium, or that more than four microspores are formed in certain angiosperms. It may well be that all the conditions mentioned represent mere adaptations.

In the lichens many-celled spores occur, which are at first always uninucleate; for example, those of Endocarpon. The embryo gametophyte is formed in the spore, which continues its growth when conditions become favorable. Each cell, however, of the multinucleate septate spore gives rise to a filament when the spore germinates. Each cell of a septate spore is comparable to a spore of Thecotheus, in which walls have not been formed until the nuclear divisions have been completed. Germination occurs in the one case before spore delimitation, and in the other case after spore delimitation. In either case, after eight nuclei are formed we are dealing with gametophyte structures. It is a matter of indifference when germination occurs, or when spore delimitation takes place, so long as the triple division has occurred. The time of spore formation is a matter of adaptation to conditions, but the essential nature of the process seems to be the same in all genuine members of the group of Ascomycetes so far studied.

SUMMARY.

1. The fruit body of Thecotheus is formed from several ascogonia and is therefore a compound apothecium.
2. The ascogenous hyphae arise from any or all of the cells of the ascogonium, and consequently the cells of the ascogonium are not connected by perforations through which the nuclei pass to enter the ascogenous hyphae.
3. The ascogenous hyphae do not in this case constitute a synkaryophytic system.
4. The asci arise from the subterminal cells of the recurved tips of the ascogenous hyphae, which cells are binucleate.
5. The ascus nucleus is formed by the fusion of these two primary ascus nuclei.
6. The ascus nucleus divides by triple division to form eight free nuclei, each of which after a period of rest and growth undergoes further division until thirty-two free nuclei are formed in the ascus.
7. Spore delimitation follows the process described by Harper.
8. Each spore is uninucleate from the start, no nuclear divisions or septa being formed.

9. The exospore is laid down not from the epiplasm but by deposition from the outer layer of the sporeplasm.

10. No evidence has been found to support the theory that the ascus is homologous with the sporangia of either the Oomycetes or the Phycomycetes.

11 The formation of the large number of spores is evidently an adaptive phenomenon, and does not interfere with the conception that the ascus is a spore mother cell.

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LITERATURE CITED.

Allen, C. E., **:04**, Chromosome reduction in *Lilium canadense*. Bot. Gazette **37**: 464–471.

——, **:05**, Nuclear division in the pollen mother cells of *Lilium canadense*. Annals of Botany **19**: 191–258.

——, **:05**, Das Verhalten der Kernsubstanzen während der Synapsis in den Pollenmutterzellen von *Lilium canadense*. Jahrb. Wiss. Bot. **42**: 72–82.

Baranetzky, J., **'72**, Entwickelungsgeschichte des *Gymnoascus Reessii*. Bot. Zeit. **30**: 145–158.

Barker, P. T. B., **:03**, The morphology and development of the ascocarp in Monascus. Annals of Botany **17**: 167–236.

——, **:03**, The development of the ascocarp in Ryparobius. Rept. British A. A. S., Southport, 849–850.

——, **:04**, Further observations on the ascocarp of Ryparobius. Rept. British A. A. S., Cambridge, 825–826.

Bauke, H., **'77**, Zur Entwickelungsgeschichte der Ascomyceten. Bot. Zeit. **35**: 314–326.

Baur, E., **'98**, Zur Frage nach der Sexualität der Collemaceen. Ber. Deutsch. Bot. Gesells. **16**: 363–367.

——, **:01**, Die Anlage und Entwickelung einiger Flechtenapothecien. Flora **88**: 319–332.

——, **:04**, Untersuchungen über die Entwickelungsgeschichte der Flechtenapothecien. Bot. Zeit. **62**: 21–44.

Berghs, J., **:04**, **:05**, La formation des chromosomes hétérotypiques dans la sporogénèse végétale. I. Depuis le spirème jusqu'aux chromosomes mûrs. La Cellule **21**: 173–188. II. Depuis la sporogonie jusqu'au spirème définitif dans la microsporogénèse de l'*Allium fistulosum*. *Idem* 383–384. III. La microsporogénèse de *Convallaria majalis*. *Idem* **22**: 43–49. IV. La microsporogénèse de *Drosera rotundifolia*, *Narthecium ossifragum*, et *Helleborus foetidus*. *Idem* 141–160.

BERLESE, A. N., **'99**, Studi citologici sui funghi. Riv. Pathol. Veg. **8**:143-152.

BERTHOLD, G., **'86**, Studien über Protoplasmamechanik . Leipzig.

BORZI, A., **'78**, Studii sulla sessualitá degli Ascomicete. Nuovo Giorn. Bot. Ital. **10**:43-78.

BOUDIER, É., **'69**, Mémoire sur les Ascobolées. Ann. Sci. Nat. Bot. V. **10**:191-268.

BLACKMAN, V. H., **:04**, On the fertilization, alternation of generations, and general cytology of the Uredineae. Annals of Botany **18**:323-373.

BLACKMAN, V. H., and FRAZER, HELEN C. J., **:05**, Fertilization in Sphaerotheca. Annals of Botany **19**:567-569.

———, **:06**, Further studies on the sexuality of the Uredineae. Annals of Botany **20**:35-48.

———, **:06**, On the sexuality and development of the ascocarp of *Humaria granulata*. Proc. Roy. Soc. London B. **77**:354-368.

BREFELD, O., **'74**, Untersuchungen aus dem Gesammtgebiete der Mykologie. Botanische Untersuchungen über Schimmelpilze. II. Penicillium. Leipzig.

BÜSGEN, M., **'82**, Die Entwicklung der Phycomycetensporangien. Jahrb. Wiss. Bot. **13**:253-285.

CARDIFF, I. D., **:06**, A study of synapsis and reduction. Bull. Torr. Bot. Club **33**:271-306

CAVARA, F., **'89**, Matériaux de mycologie lombarde. Rev. Mycol. **12**:173-193.

———, **:05**, Causeries mycologiques. Ann. Mycol. **3**:362-365.

CHRISTMAN, A. H., **:05**, Sexual reproduction in the rusts. BOT. GAZETTE **19**:267-275.

CLAUSSEN, P., **:05**, Zur Entwickelungeschichte der Ascomyceten. Boudiera. Bot. Zeit. **63**:1-28.

CROUAN, FRÈRES, **'57**, Note sur quelques Ascobolus nouveaux et sur une espèce nouvelle de Vibrissea. Ann. Sci. Nat. Bot. IV. **7**:173-178.

DALE, Miss E., **:03**, Observations on Gymnoascaceae. Annals of Botany **17**:571-596.

DANGEARD, P., **'94**, **'95**, La reproduction sexuelle des Ascomycètes. Le Botaniste **4**:21-58.

———, **'94**, **'95**, La truffe. Recherches sur son développement, sa structure, sa reproduction sexuelle. *Idem* 63-87.

———, **'96**, **'97**, Second mémoire sur la reproduction sexuelle des Ascomycètes. *Idem* **5**:245-284.

———, **:03**, Sur le nouveau genre Protascus. *Idem* **9**:23-25.

———, **:03**, Sur le genre Ascodesmis. *Idem* 33-35.

———, **:03**, Nouvelles considérations sur la reproduction sexuelle des champignons supérieurs. *Idem* 35-46.

DARBISHIRE, O. V., **'99**, Ueber die Apothecienentwicklung der Flechte *Physcia pulverulenta*. Jahrb. Wiss. Bot. **34**:329-345.

DAVIS, B. M., **:03**, Oogenesis in Saprolegenia. BOT. GAZETTE **35**:233-249, 320-349.

DeBary, A., **'63**, Ueber die Fruchtentwicklung der Ascomyceten. Leipzig.

———, **'70**, Eurotium, Erysiphe, Cicinnobolus, nebst Bemerkungen über die Geschlechtsorgane der Ascomyceten. Beitr. Morph. u. Phys. der Pilze **3**: 1–95.

Eidam, E., **'83**, Beitrag zur Kenntniss der Entwicklung der Gymnoasceen. Cohn's Beitr. Biol. Pflanz. **3**: 267–305.

———, **'83**, Zur Kenntniss der Entwicklung bei den Ascomyceten. *Idem* 377–433.

Faull, J. H., **:05**, Development of ascus and spore formation in Ascomycetes. Proc. Boston Soc. Nat. Hist. **32**: 77–114.

———, **:06**, A preliminary note on ascus and spore formation in the Laboulbeniaceae. Science N. S. **23**: 152–153.

Fuisting, W., **'67**, Zur Entwickelungsgeschichte der Pyrenomyceten. Bot. Zeit. **25**: 177–181, 185–189, 193–198.

Fünfstück, M., **:02**, Der gegenwartige Stand der Flechtenkunde. Ber. Deutsch. Bot. Gesells. **20**: (62)-(77).

Gilkinet, A., **'74**, Recherches morphologiques sur les Pyrénomycètes. Bull. Acad. Roy. Belgique II. **37**: —. (pp. 28).

Gjurasin, S., **'93**, Über die Kernteilung in den Schlauchen von *Peziza vesiculosa*. Ber. Deutsch. Bot. Gesells. **2**: 113–117.

Grégoire, V., **:04**, Le réduction numérique des chromosomes et les cinèses de maturation. La Cellule **21**: 297–314.

Guilliermond, M. A., **:03**, Contribution à l'étude de l'épiplasme des Ascomycètes, Compt. Rend. Acad. Sci. Paris **136**: 253–255.

———, **:03**, Contribution à l'étude cytologique des Ascomycètes. *Idem* 938-939, 1088.

———, **:03**, Nouvelles recherches sur l'épiplasme des Ascomycètes. *Idem* 1487–1489.

———, **:03**, Contributions à l'étude de l'épiplasme des Ascomycètes et recherches sur les corpuscules métachromatiques des champignons. Ann. Mycol. **1**: 201–215.

———, **:04**, Contributions à l'étude de la formation des asques et de l'épiplasme des Ascomycètes. Rev. Gén. Bot. **16**: 1–65.

———, **:04**, Recherches sur la karyokinèse chez des Ascomycètes. *Idem* 129-143.

———, **:04**, Sur la karyokinèse de *Peziza rutilans*. Compt. Rend. Soc. Biol. **56**: 412.

———, **:05**, Sur la nombre des chromosomes chez les Ascomycètes. *Idem* **58**: —.

———, **:05**, Remarques sur la karyokinèse des Ascomycètes. Ann. Mycol. **3**: 344–361.

———, **:05**, Recherches sur la germination des spores et la conjugaison chez les levures. Rev. Gén. Bot. **17**: 337–377.

Harper, R. A., **'95**, Die Entwicklung des Peritheciums bei *Sphaerotheca castagnei*. Ber. Deutsch. Bot. Gesells. **13**: 475–481.

———, **'95**, Beiträge zur Kenntniss der Kernteilung und Sporenbildung im Ascus. *Idem* (67)-(78).

HARPER, R. A., **'96**, Ueber das Verhalten der Kerne bei der Fruchtentwicklung einiger Ascomyceten. Jahrb. Wiss. Bot. **29**:655-685.

———, **'97**, Kernteilung und freie Zellbildung im Ascus. *Idem* **30**:249-284.

———, **'99**, Cell division in sporangia and asci. Annals of Botany **13**:467-524.

———, **:00**, Sexual reproduction in *Pyronema confluens* and the morphology of the ascocarp. *Idem* **14**:321-400.

———, **:05**, Sexual reproduction and the organization of the nucleus in certain mildews. Publ. Carnegie Institution, Washington, no. 37, pp. 92.

HARTOG, M., **'88**, Recent researches on the Saprolegnieae. A critical abstract of ROTHERT'S results. Annals of Botany **2**:201-216.

———, **'95**, On the cytology of the vegetative and reproductive organs of the Saprolegnieae. Trans. Royal Irish Acad. **30**:649-708.

———, **'96**, The cytology of Saprolegnia. Annals of Botany **10**:98-100.

———, **'99**, The alleged fertilization in the Saprolegnieae. *Idem* **13**:447-459.

HENNINGS, P., **:03**, Einige deutsche dungbewohnende Ascomyceten. Hedwigia Beibl. **42**:181-185.

HUMPHREY, J. E., **'92**, Saprolegniaceae of the United States. Trans. Am. Phil. Soc. **17**:63-148.

IKENO, S., **:01**, Studien über die Sporenbildung bei *Taphrina Johansoni* Sad. Flora **88**:229-237.

———, **:03**, Die Sporenbildung von Taphrina-Arten. *Idem* **92**:1-31.

———, **:03**, Ueber die Sporenbildung und systematische Stellung von *Monascus purpureus* Went. Ber. Deutsch. Bot. Gesells. **21**:259-269.

JANCZEWSKI, E,. DEG. **'72**, Recherches morphologiques sur l'*Ascobolus furfuraceus*. Ann. Sci. Nat. Bot. V. **15**:197-214.

JUEL, H. O., **'97**, Die Kernteilungen in den Pollenmutterzellen von *Hemerocallis fulva* und die bei denselben auftretenden Unregelmässigkeiten. Jahrb. Wiss. Bot. **30**:205-226.

———, **:00**, Beiträge zur Kenntniss der Tetradenteilung. *Idem* **35**:626-659.

———, **:00**, Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei der Gattung Antennaria. Konigl. Svensk. Vetensk. Akad. Handl. **33**:no. **5**. pp. 59.

———, **:02**, *Taphridium* Lagerh. und Juel. Eine neue Gattung der Protomycetaceen. Konigl. Svensk. Vetensk. Akad. Handl. **27**:no. 16. pp. 29.

———, **:02**, Ueber Zellinhalt, Befruchtung und Sporenbildung bei Sporenbildung bei Dipodascus. Flora **91**:47-55.

———, **:05**, Die Tetradenteilungen bei Taraxacum und anderen Chicorieen. Konigl. Svensk. Vetensk. Akad. Handl. **39**:no. 4. pp. 21.

KIHLMAN, O., **'83**, Zur Entwicklungsgeschichte der Ascomyceten. Acta Soc. Sci. Fenn. **13**:Sonderabdr. 1-43.

KRABBE, G., **'83**, Morphologie und Entwickelungsgeschichte der Cladoniaceen. Ber. Deutsch. Bot. Gesells. **1**:64-77.

———, **'95**, Beiträge zur Kenntniss der Ascomyceten. Leipzig.

KUYPER, H. P., :**04**, Die Perithecium-Entwicklung von *Monascus purpureus* Went. und *Monascus Barkeri* Dang., und die systematische Stellung dieser Pilze. Ext. du Recueil des Travaux Bot. Neer.

———, :**05**, Die Peritheciumentwickelung von *Monascus purpureus* Went. und *Monascus Barkeri* Dang. so wie die systematische Stellung dieser Pilze. Ann. Mycol. **3**:32–81.

LINDAU, G., '**88**, Ueber die Anlage und Entwickelung einiger Flechtenapothecien. Flora **62**:451–489.

———, '**89**, Beiträge zur Kenntniss der Gattung Gyrophora. Festsch. f. Schwendener. Berlin.

MAIRE, R., :**03**, Recherches cytologiques et taxonomiques sur les Basidiomycètes. Bull. Soc. Mycol. France **18**:1–209.

———, :**03**, Recherches cytologiques sur les *Galactinia succosa.* Compt. Rend. Acad. Sci. Paris **137**:769–771.

———, :**03**, La formation des asques chez les Pezizes et l'évolution nucléaire des Ascomycètes. Compt. Rend. Soc. Biol. **55**:1401.

———, :**04**, Remarques sur la cytologie de quelques Ascomycètes. *Idem* **56**:86.

———, :**04**, Sur les divisions nucleaires dans l'asque de la morelle et de quelques autres Ascomycètes. *Idem* 822.

———, :**05**, La mitose hétérotypique chez les Ascomycètes. Compt. Rend. Acad. Sci. Paris **149**:950–952.

———, :**05**, La mitose hétérotypique et la signification des protochromosomes chez les Basidiomycètes. Compt. Rend. Soc. Biol. **58**:726.

———, :**05**, Recherches cytologiques sur quelques Ascomycètes. Ann. Mycol. **3**: 123–154.

MIYAKI, K., :**05**, Ueber Reduktionsteilung in den Pollenmutterzellen einiger Monokotylen. Jahrb. Wiss. Bot. **42**:83–120.

MURBECK, S., :**01**, Parthenogenetische Embryobildung in der Gattung Alchemilla. Lunds. Univ. Årssk. **36**:no. 7. pp. 41.

NICHOLS, Miss M. A., '**96**, The morphology and development of certain pyrenomycetous fungi. BOT. GAZETTE **22**:301–328.

NICHOLS, Miss S. P., :**04**, The nature and origin of the binucleated cells in some Basidiomycetes. Trans. Wis. Acad. Sci. **15**:30–70.

OLIVE, E. W., :**05**, The morphology of *Monascus purpureus*. BOT. GAZETTE **39**:50–60.

OLTMANNS, F., :**87**, Ueber die Entwickelung der Perithecien in der Gattung Chaetomium. Bot. Zeit. **45**:196–199, 210–218, 250–254.

OVERTON, J. B., :**04**, Ueber Parthenogenesis bei *Thalictrum purpurascens.* Ber. Deutsch. Bot. Gesells. **22**:274–283.

———, :**05**, Über Reduktionsteilung in den Pollenmutterzellen einiger Dicotylen. Jahrb. Wiss. Bot. **42**:121–153.

PATOUILLARD, N., Tabulae analyticae fungorum 1:74. Poligny.

POPTA, M. L., '**99**, Beitrag zur Kenntniss der Hemiasci. Flora **86**:1–46.

PRINGSHEIM, N., '**51**, Die Entwickelungsgeschichte der *Achlya prolifera*. Nov. Act. Caes. Leop. Carol. Nat. Cur. **23**:397–460.

RAMLOW, G., '**96**, Zur Entwicklungsgeschichte von *Thelebolus stercoreus*. Bot. Zeit. **64**:85–99.

REHM, H., '**96**, Rabenhorst's Kryptogamen-Flora IV. Pilze **3**:1000.

ROSENBERG, O., :**05**, Zur Kenntniss der Reducktionsteilung im Pflanzen. Bot Not. **1905**: 1–24.

ROTHERT, W., '**88**, Die Entwickelung der Sporangien bei den Saprolegnieen. Cohn's Beitr. Biol. Pflanzen **5**:291–349.

SADEBECK, R., '**93**, Die parasitischen Exoasceen. Jahrb. Hamburg. Wiss. Anstalt **10**:no. 2. pp. 110.

———, '**95**, Einige neue Beobachtungen und Kritische Bemerkungen über die Exoascaceae. Ber. Deutsch. Bot. Gesells. **13**:265–280.

SAPPIN-TROUFFY, '**96**, '**97**, Note sur la place du *Protomyces macrosporus* dans la classification. Le Botaniste **5**:285–288.

SCHULTE, F., :**05**, Zur Anatomie der Fletchtengattung Usnea. Beih. Bot. Centralb. **18**:1–22.

STAHL, E., '**77**, Beiträge zur Entwickelungsgeschichte der Flechte. I & II. Leipzig.

STRASBURGER, E., '**80**, Zellbildung und Zellteilung. Jena.

———, :**04**, Ueber Reduktionsteilung. Sitzungsber. Kön. Preuss. Akad. Wiss. **18**:587 614.

———, :**04**, Die Apogamie der Eualchemillen und allgemeine Gesichtspunkte, die sich aus ihr geben. Jahrb. Wiss. Bot. **41**:88–164.

———, :**05**, Typische und allotypische Kernteilung, Ergebnisse und Erörterungen. Jahrb. Wiss. Bot. **42**:1–71.

SWINGLE, D. B., :**03**, Formation of the spores in the sporangia of *Rhizopus nigricans* and of *Phycomyces nitens*. U. S. Dept. Agr., Bureau Plant Ind., Bull. 37:1–40.

TISCHLER, G., :**06**, Über die Entwicklung des Pollens und der Tapetenzellen bei Ribes-Hybriden. Jahrb. Wiss. Bot. **42**:545–578.

———, :**06**, Ueber die Entwicklung der Sexualorgane bei einem sterilen Bryonia-Bastard. Ber. Deutsch. Bot. Gesells. **24**:83–96.

TROW, A. H., '**05**, The karyology of Saprolegnia. Annals of Botany **9**:609–652.

———, '**99**, Observations on the biology and cytology of a new variety of *Achlya americana*. Annals of Botany **13**:131–179.

TULASNE, R. & C., '**65**, Selecta Fungorum Carpologia **3**:197–198.

———, '**66**, Note sur les phénomènes de copulation que présentent quelques champignons. Ann. Sci. Nat. Bot. V. **6**:211–220.

VAN TIEGHEM, P., '**75**, Sur le développement du fruit des Chaetomium et la prétendue sexualité des Ascomycètes. Compt. Rend. Acad. Sci. Paris **81**: 1110–1113.

———, '**76**, Sur le développement du fruit des Ascodesmis. Bull. Soc. Bot. France **23**:271–279.

VAN TIGHEM, P, '**76**, Nouvelle observations sur le développement du fruit et sur la prétendue sexualité des Basidiomycètes et des Ascomycètes. *Idem* 99–105.

———, '**76**, Nouvelles observations sur le développement du périthèce des Chaetomium. *Idem* 364–366.

———, '**77**, Sur le développement de quelques Ascomycètes. *Idem* **24**:96–105, 159–169, 203-206, 206–210.

WAINO, E. A., '**90**, Étude sur la classification naturelle et la morphologie des lichens du Brésil. Helsingfors.

———, '**97**, '**98**, Monographia Cladoniarum universalis. Acta. Soc. Fauna et Flora Fennica **14**: 1–268.

WILLE, N., '**86**, Ueber die Entwickelungsgeschichte der Pollenkerne der Angiospermen und das Wachstum der Membranen durch Intussusception. Christiania.

WORONIN, M., '**66**, Zur Entwickelungsgeschichte des *Ascobotus pulcherrimus* und einiger Pezizeen. Beitr. Morph. u. Phys. Pilze **2**: 1–11.

———, '**70**, *Sphaeria lemaneae, Sordaria carpophila, S. fimiseda, Arthrobotrys oligospora.* Beitr. Morph. u. Phys. Pilze **3**: 1–36.

ZUKAL, H., '**86**, Mycologische Untersuchungen. Denk. Kais. Akad. Wiss. Wien **51**:21–36.

EXPLANATION OF PLATES XXIX AND XXX.

All drawings were made with the aid of a Bausch and Lomb camera lucida, together with a Bausch and Lomb $\frac{1}{12}$ oil-immersion lens. Plate XXX has been reduced one-third in reproduction.

PLATE XXIX.

FIG. 1. Section of young ascocarp showing portions of ascogonia, whose cells are already multinucleate.

FIG. 2. Median section of an older ascocarp showing ascogonia, young ascogenous hyphae, and paraphyses.

FIG. 3. Median vertical section showing structure of a nearly mature ascocarp.

FIG. 4. Section showing young ascogenous hypha; the terminal cell is uninucleate and the sub-terminal cell, which is to form the ascus, is binucleate.

FIG. 5. Young ascus showing fusion nucleus with two nucleoli.

FIG. 6. Portion of an ascus at time of spore delimitation, showing nuclear beak with a system of astral rays; a young spore is also shown, whose plasma membrane is completed.

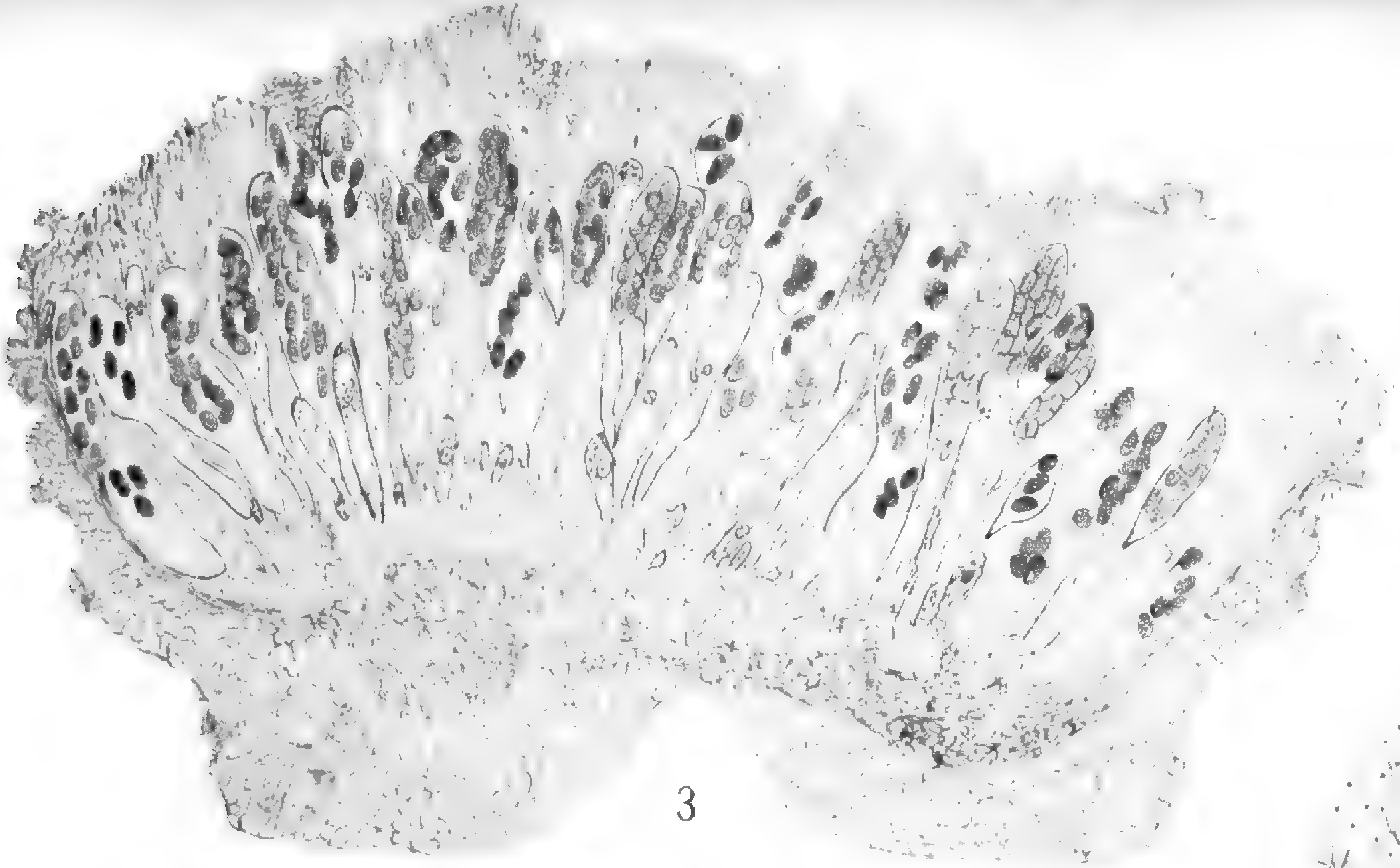
PLATE XXX.

FIG. 7. Young ascus showing primary fusion nucleus with one nucleolus.

FIG. 8. Ascus with two nuclei.

FIG. 9. Ascus with four nuclei.

FIG. 10. Ascus with eight nuclei.



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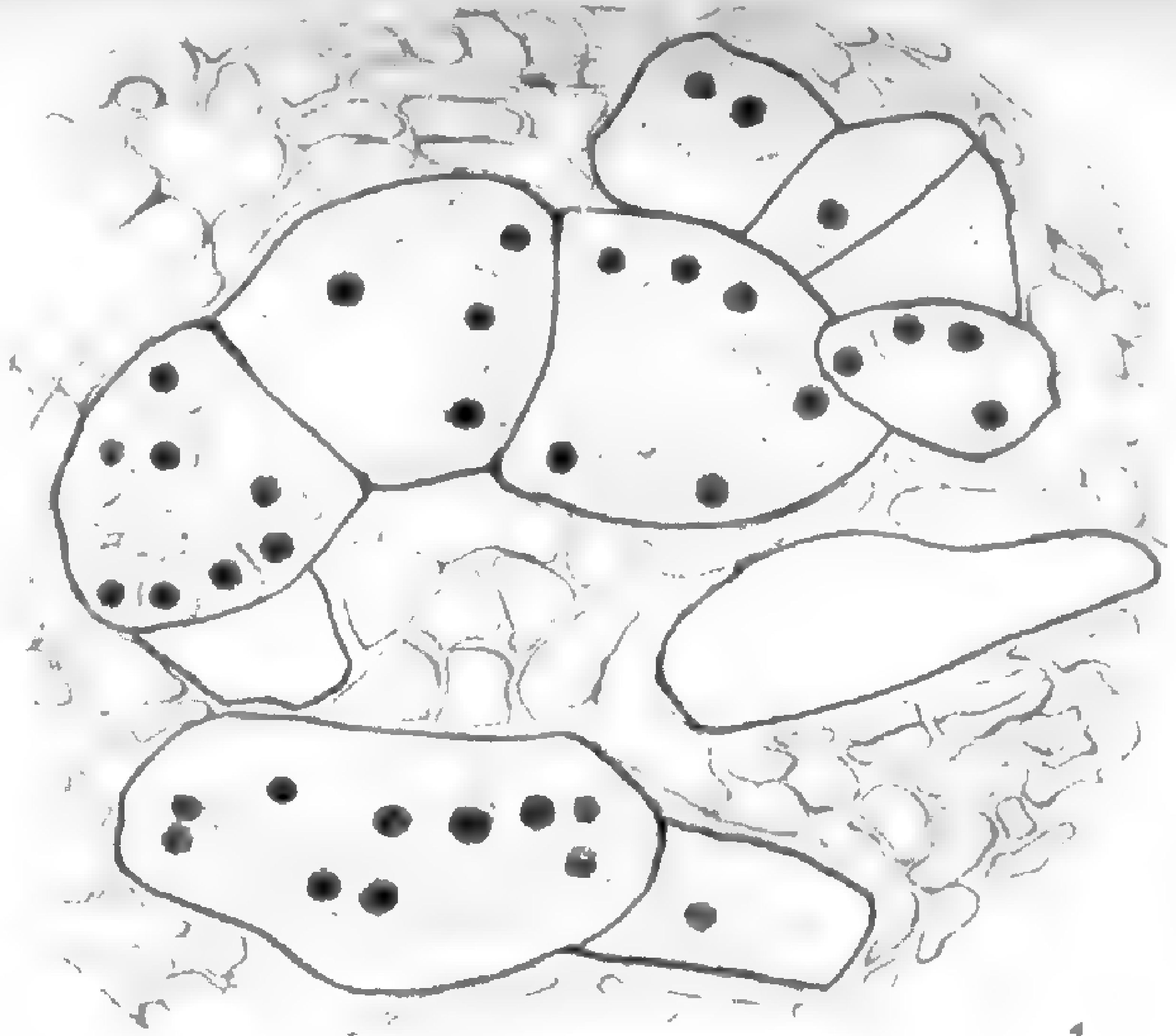

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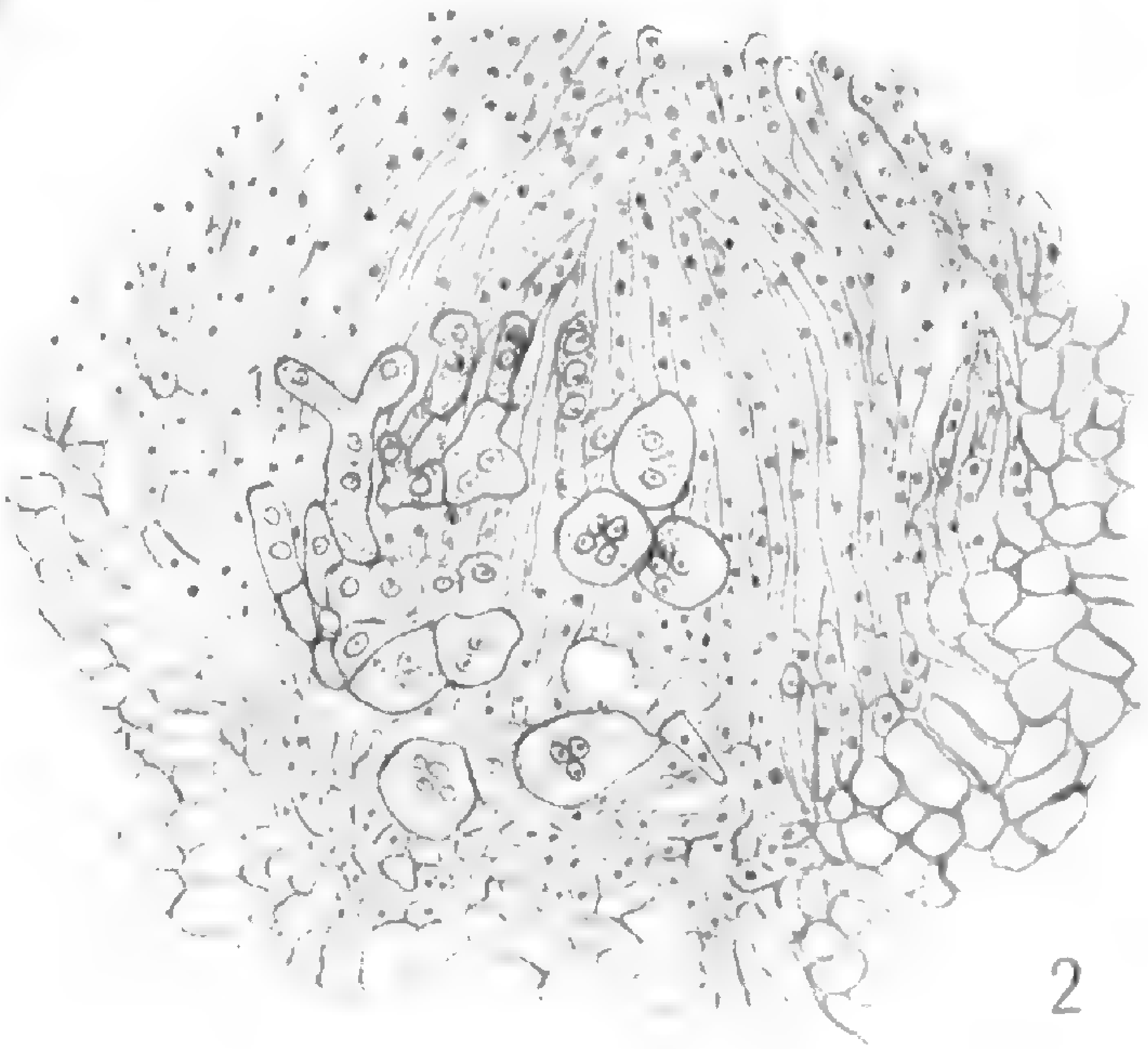

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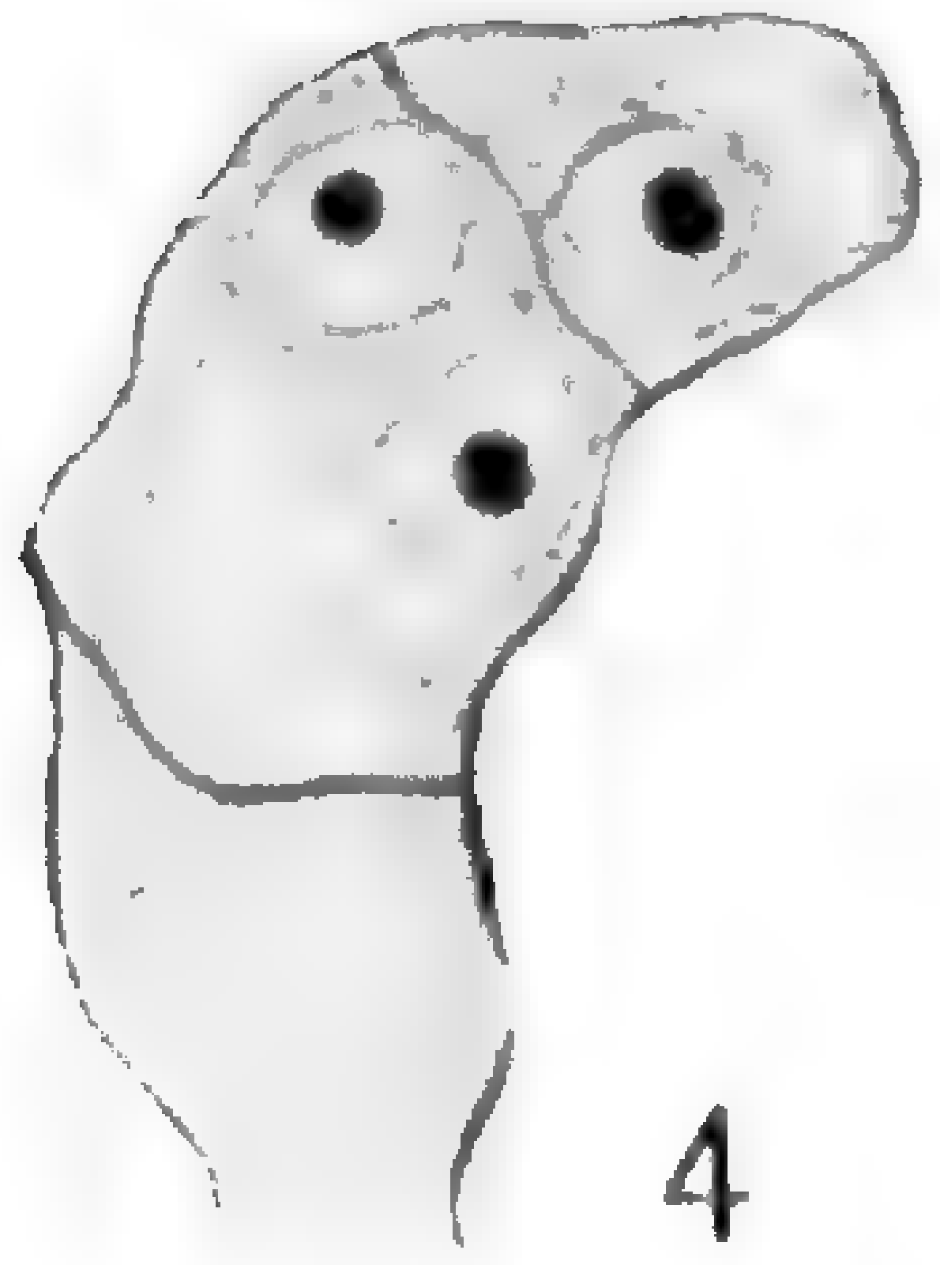

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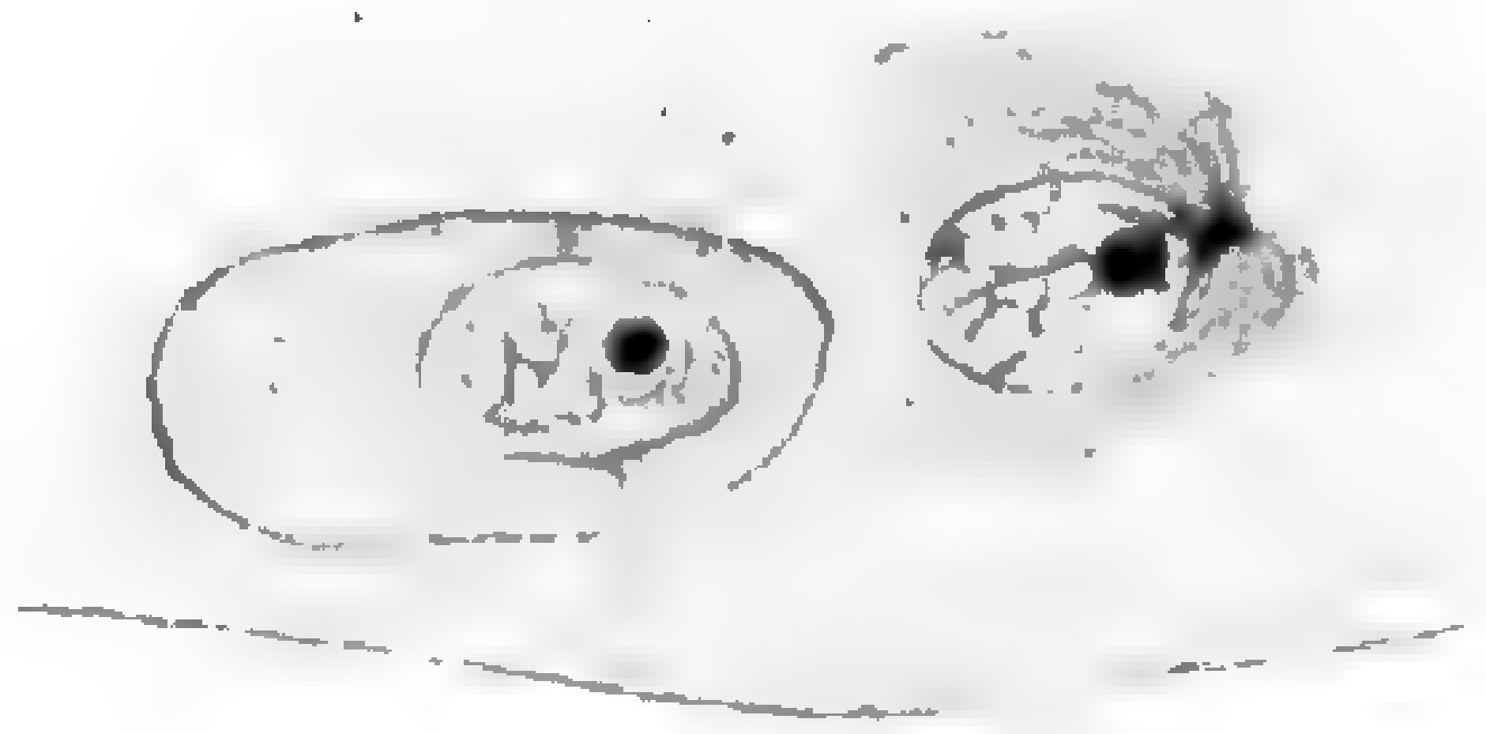

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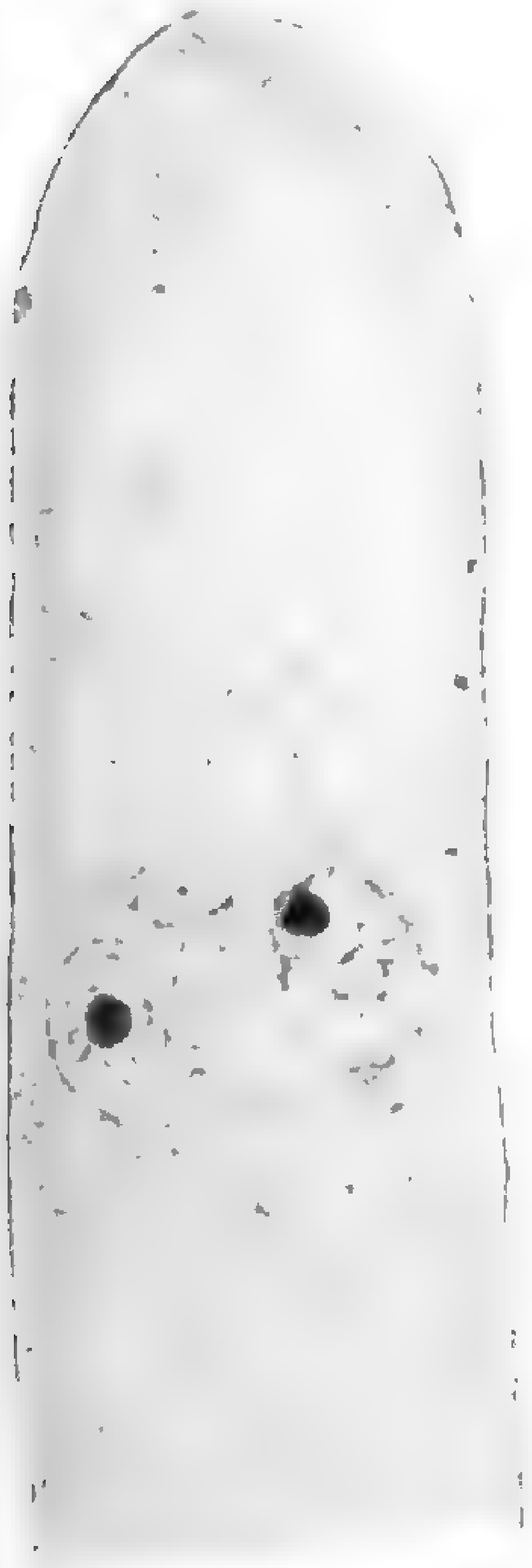
OVERTON on THECOTHEUS



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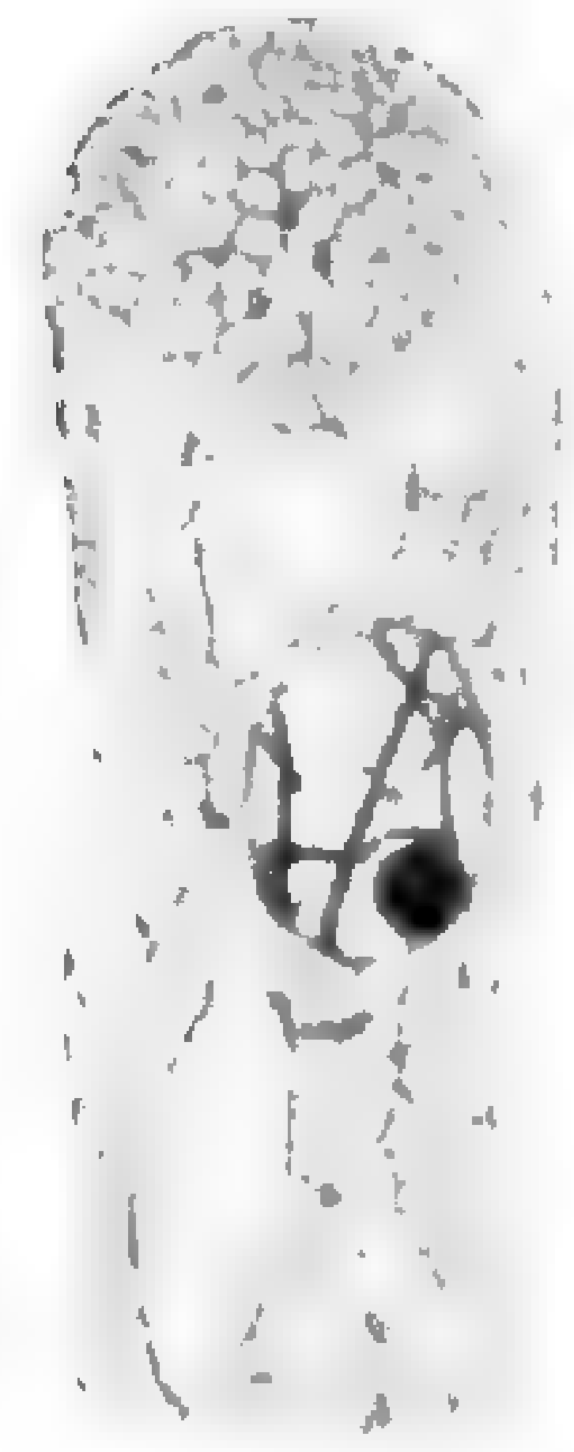

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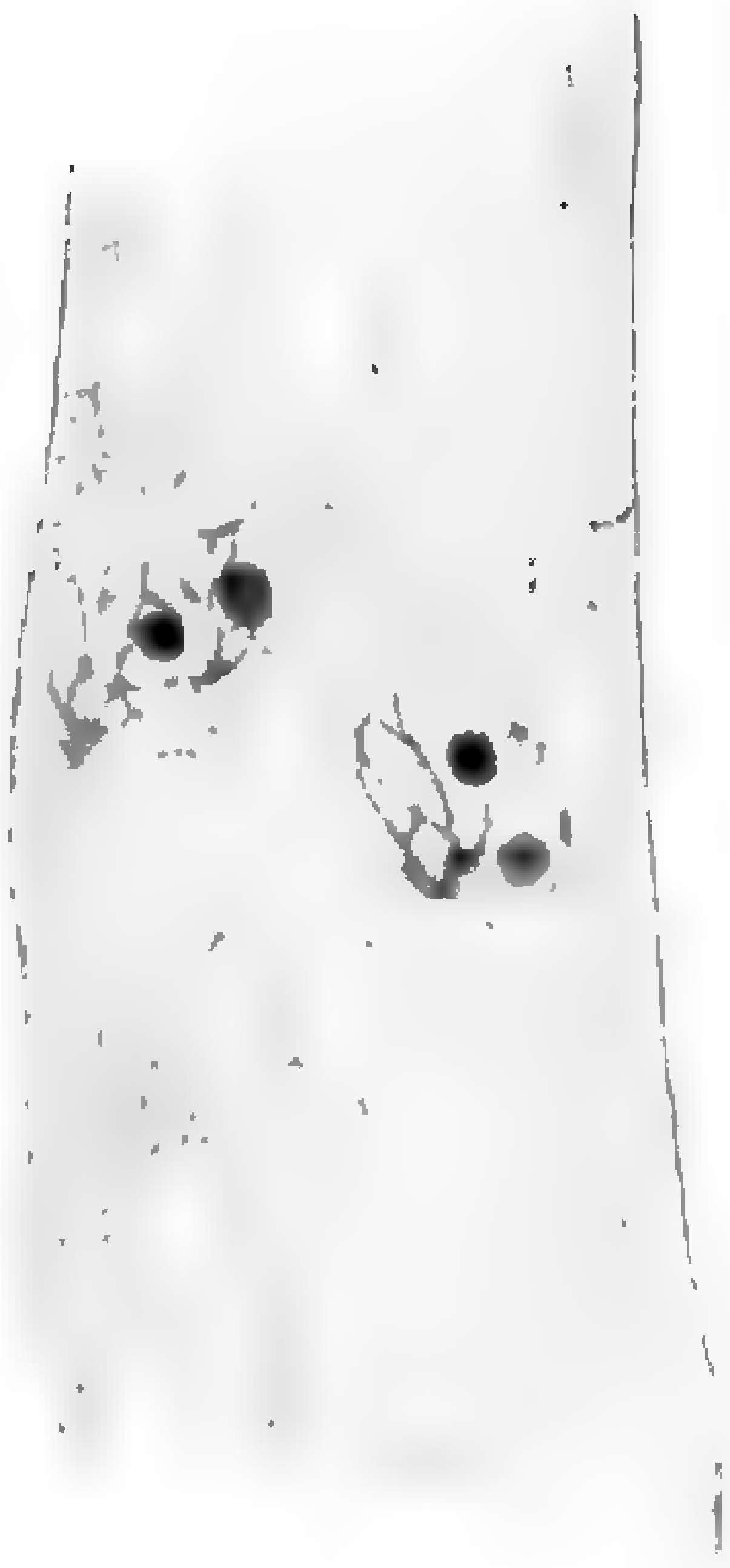

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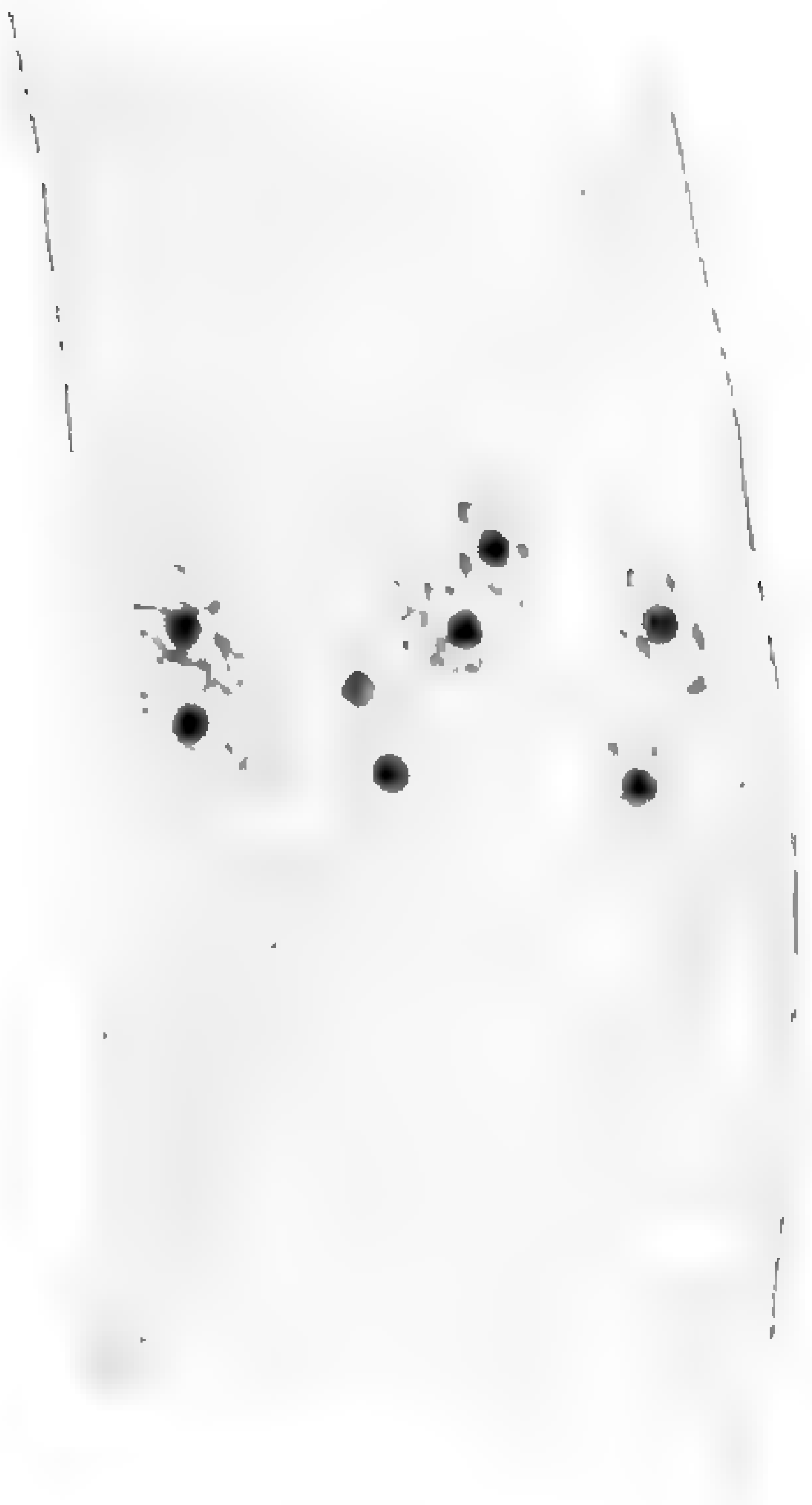

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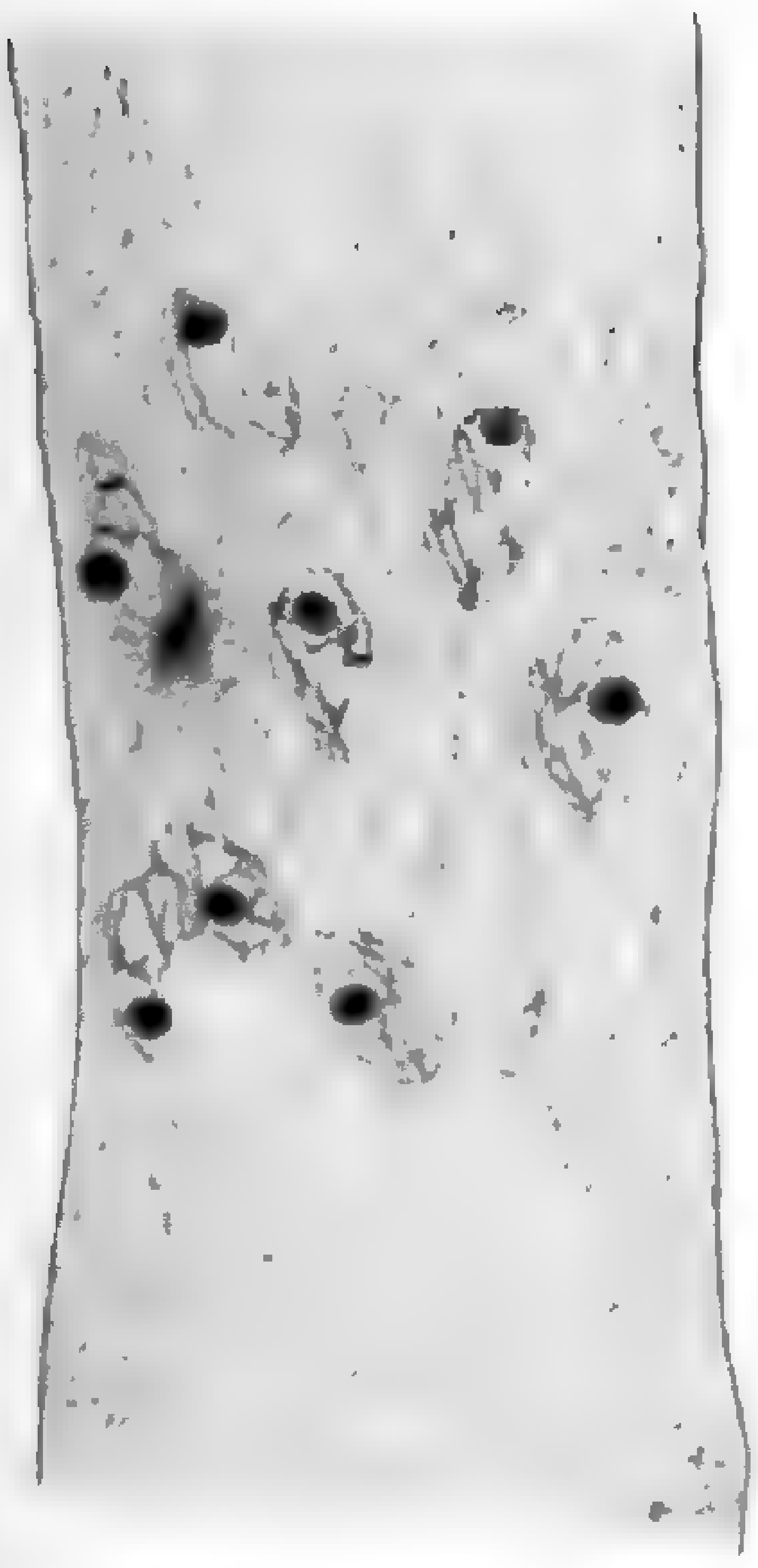

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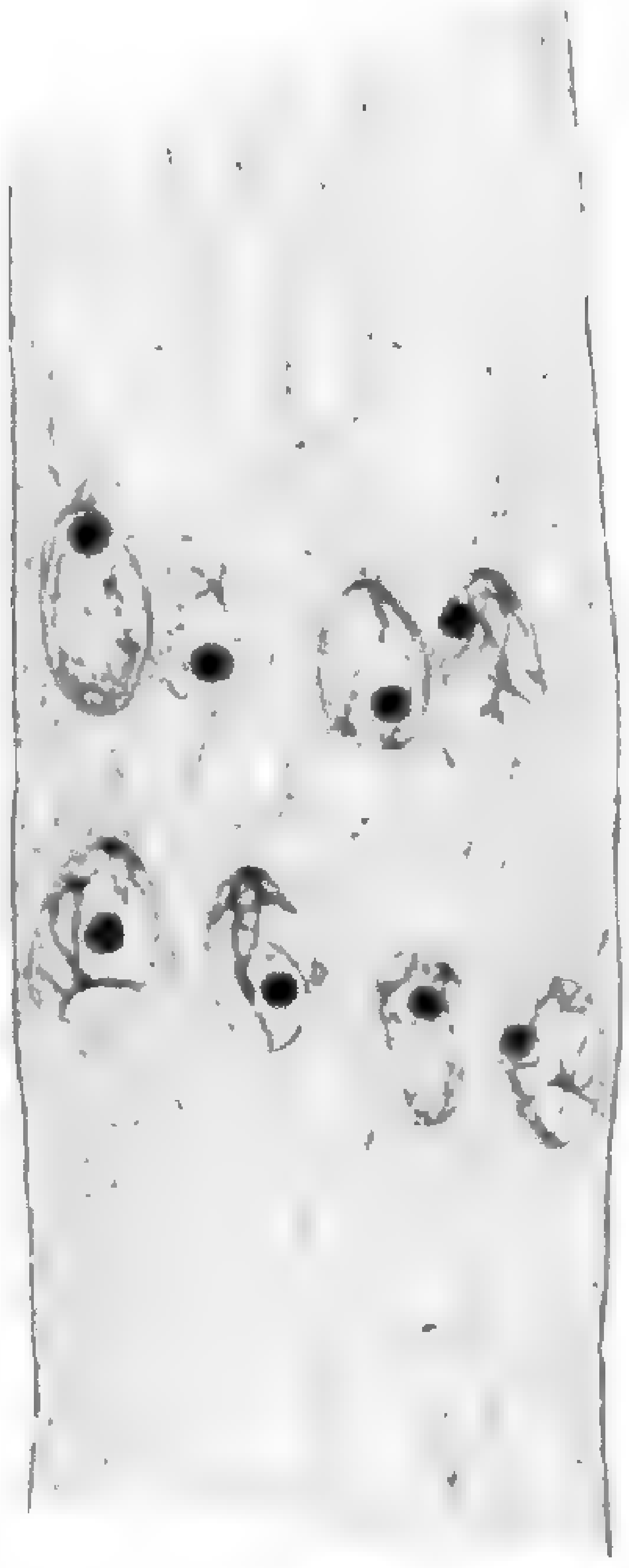

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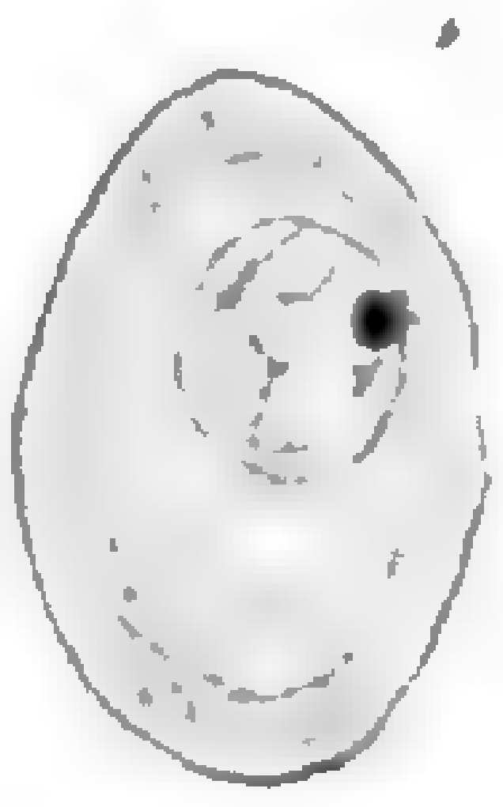

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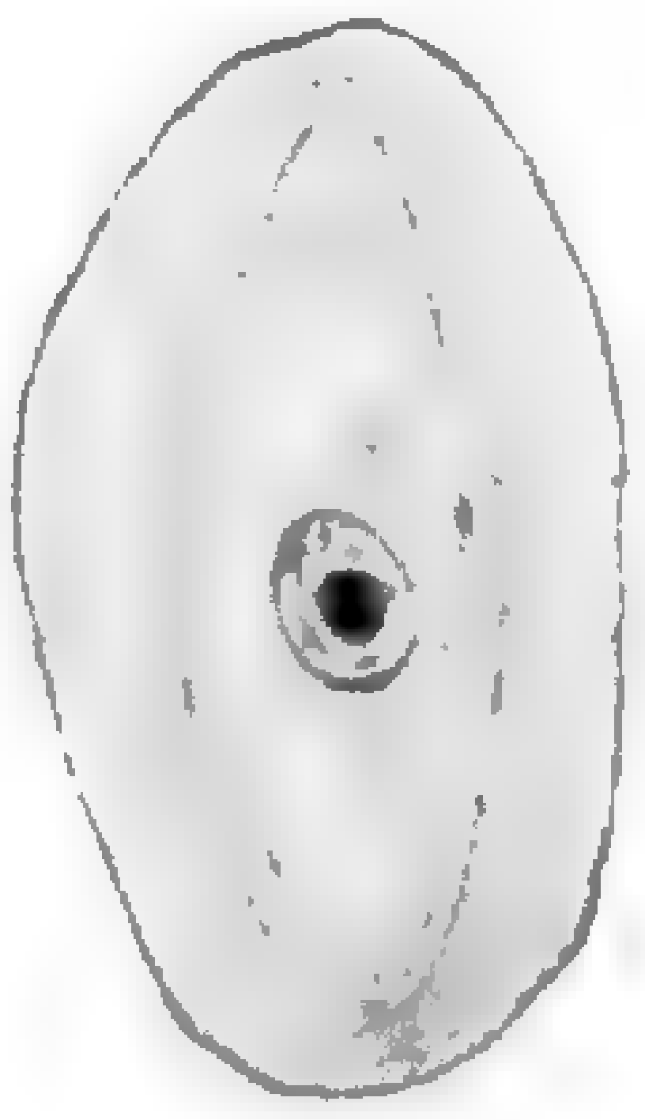

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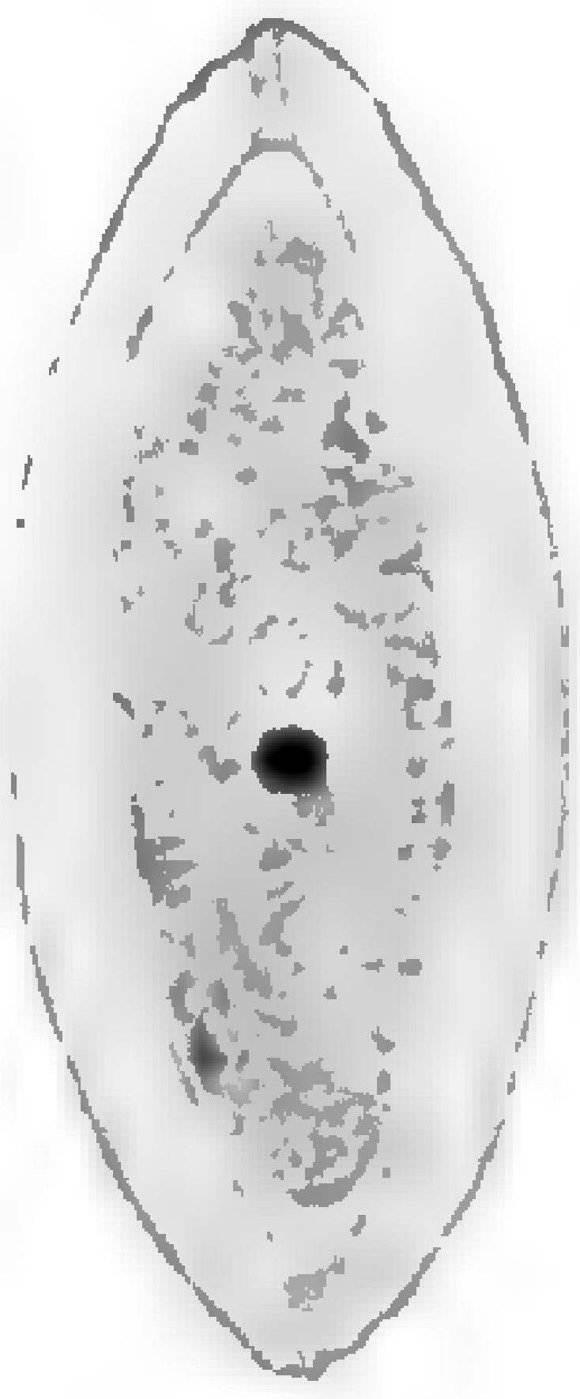

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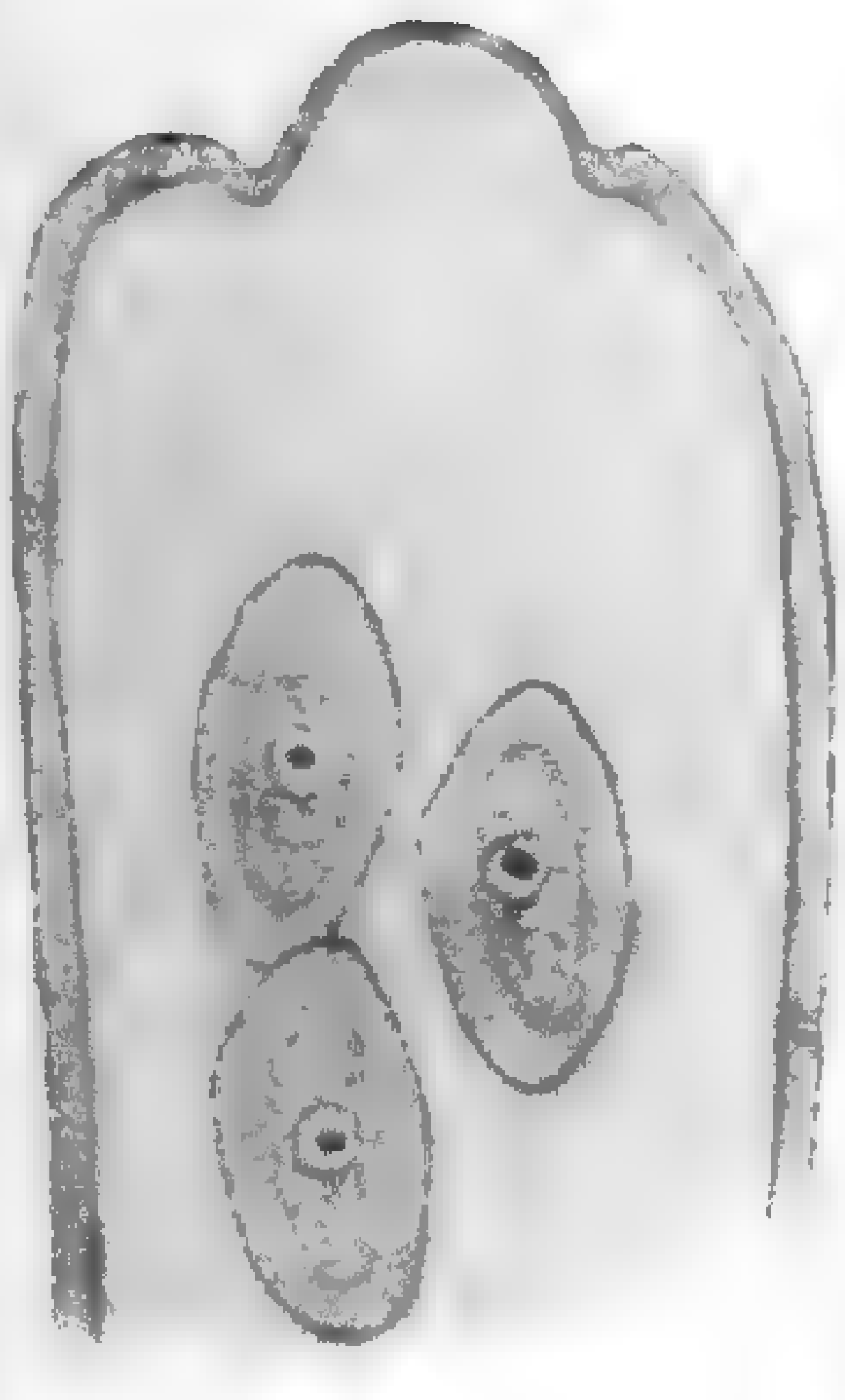

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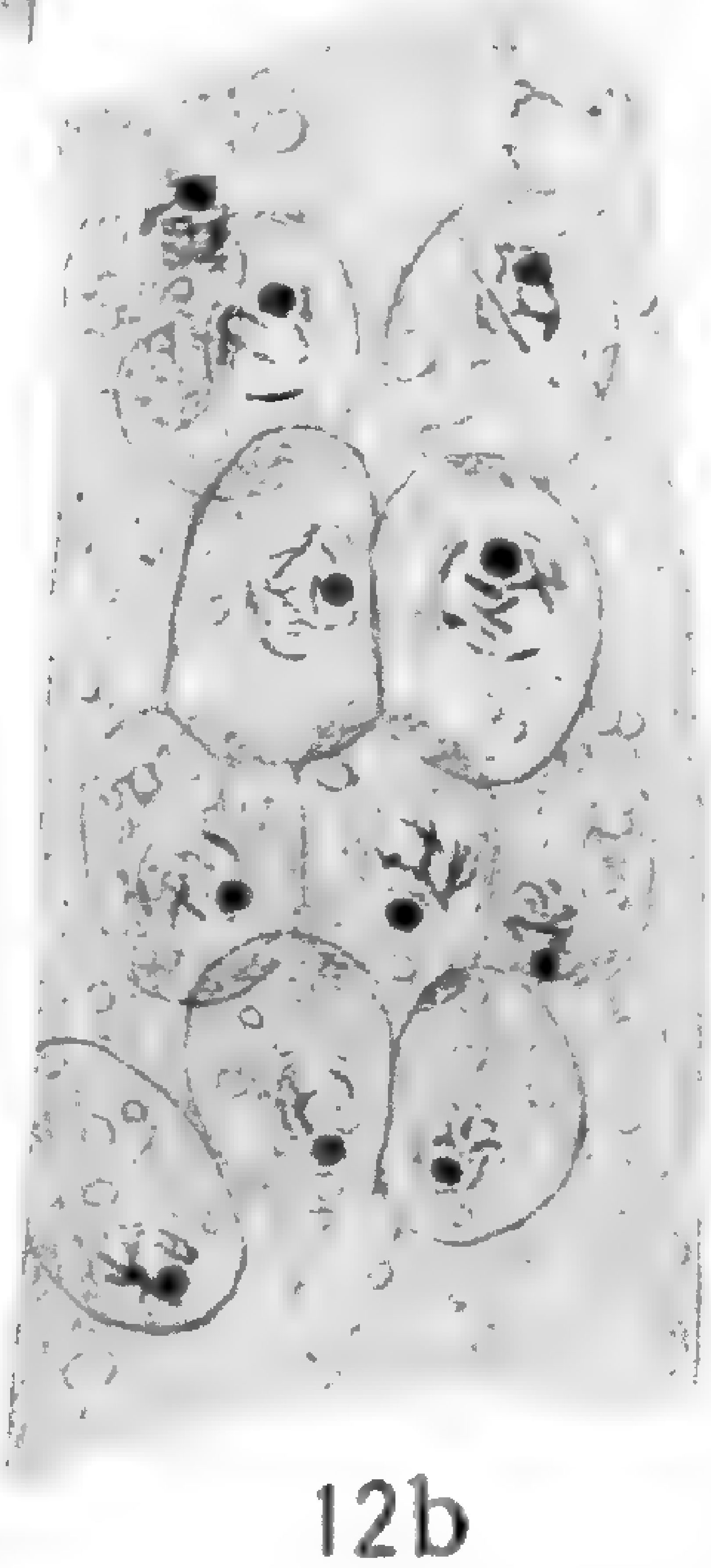

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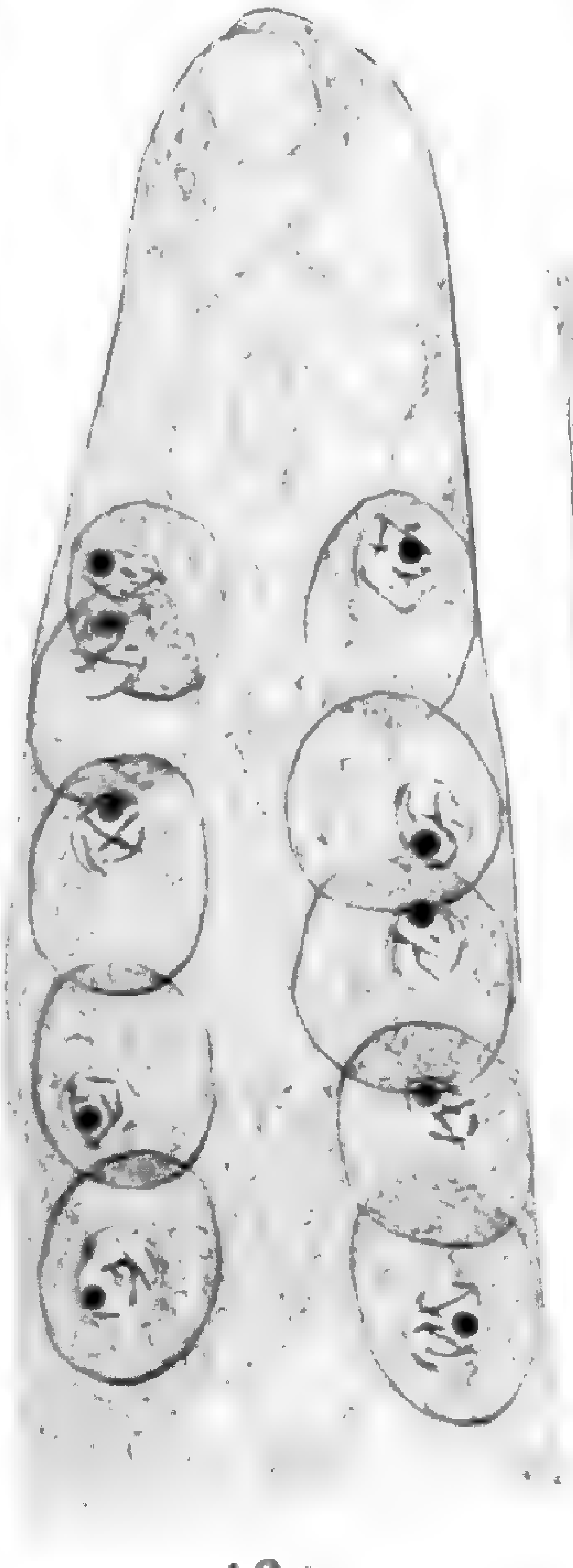

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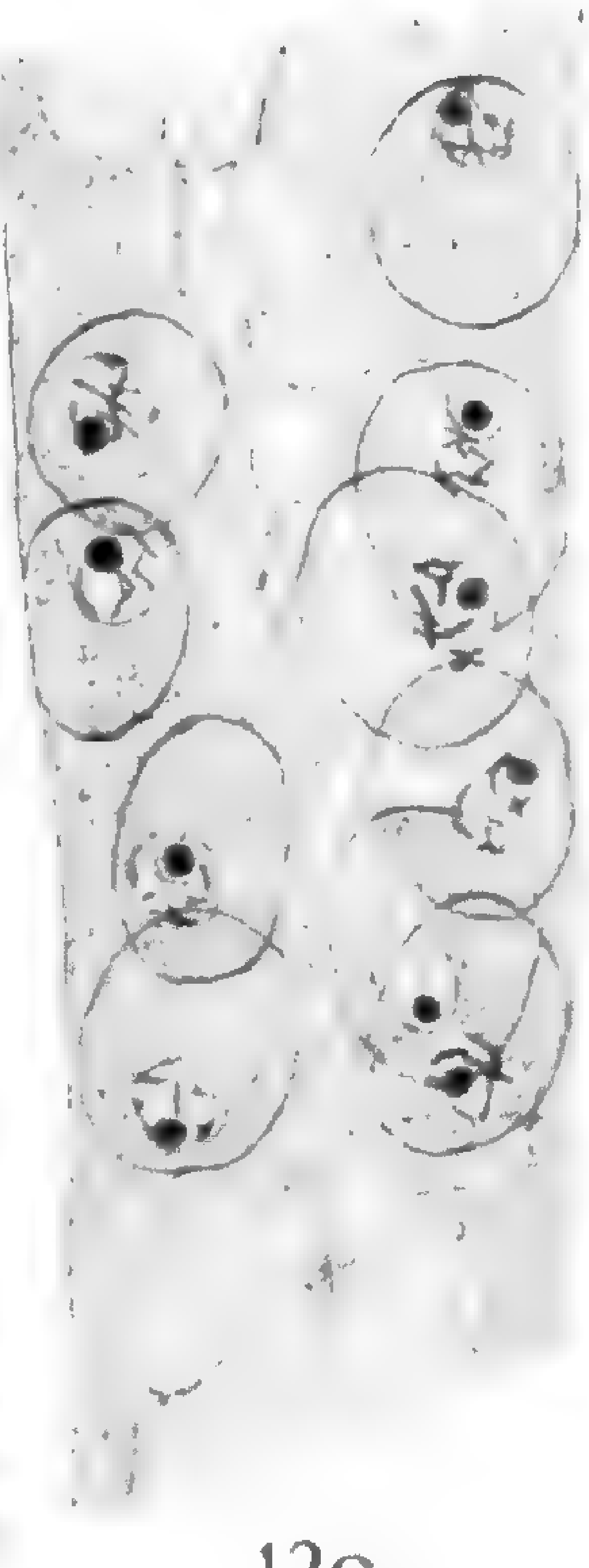

12c

OVERTON on THECOTHEUS

CURRENT LITERATURE.

BOOK REVIEWS.

The Vienna Congress.

THE PROCEEDINGS of the Congress of 1905 have recently appeared from the press of FISCHER (Jena), apparently published by the Local Committee.[1] At the same time there is published from the same house a volume containing the "scientific results" of the Congress as *Publications scientifiques de l'Association internationale des botanistes*.[2] The volumes have been distributed gratuitously to all members of the Congress, and are presumably for sale by the publisher; but the price is not stated.

The volume of *Verhandlungen* contains an account of the organization of the Congress and its daily proceedings in general sessions; the various excursions before and after the meetings; the botanical exposition (illustrated); but the greater part of the space (182 out of 262 pages) is devoted to an account of the meetings of the section for the revision of the laws of nomenclature. Here one finds not merely the *procès verbal*, but a list of the delegates and the institutions represented, an account of the discussions based on stenographic and other notes, and the votes on each question. Then follows, with double pagination, evidently for separate publication: (1) a concordance of the adopted rules with the Paris Code; (2) the revised code for the vascular plants, printed in French, English, and German; (3) a list of the names to be preserved as exceptions to the strict rule of priority; and (4) a thorough analytical index. This section of the report shows the painstaking care of M. JOHN BRIQUET, the general secretary, to whose devotion, skill, and knowledge so much of the success of the nomenclature commission was due.

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[1] Verhandlungen des internationalen botanischen Kongresses in Wien 1905. Actes du congrès international de botanique à Vienne (Autriche) 1905. Herausgegeben im Namen des Organisations-Komittees für den Kongress von R. VON WETTSTEIN und J. WIESNER als Präsidenten und A. ZALHBRUCKNER als General-Sekretär. Redigiert VON J. BRIQUET (Genf), A. GINZBERGER, V. SCHIFFNER, TH. V. WEINZIRL, R. V. WETTSTEIN und A. ZAHLBRUCKNER (Wein). Imp. 8vo. pp. vi+262. *figs. 7.* Jena: G. Fischer. 1906.

[2] Publications scientifiques de l'Association internationale des botanistes. I. Résultats scientifiques du congrès international de botanique à Vienne, 1905. Wissenschaftliche Ergebnisse des internationalen botanischen Kongresses Wien 1905. Herausgegeben im Namen des Organisations-Komittees für den Kongress von R. VON WETTSTEIN und J. WIESNER als Präsidenten und A. ZALHBRUCKNER als General-Sekretär. Redigiert von P. J. LOTSY, General-Sekretär des Ass. Int. des Bot. Imp. 8vo. pp. vi+446. *pls. 3. map 1. figs. 58.* Jena: G. Fischer. 1906.

It seems a bit invidious to distinguish the other volume as *Résultats scientifiques;* but it may pass as a conventional title. The four hundred odd pages are occupied by the formal addresses, and papers volunteered for the Congress, twenty-six in number. They are therefore of unequal quality and of different character. Some are general summaries of the present status of important divisions of botanical science; others are special and technical. Only one comes from America—"A classification of Uredineae based on structure and development," by Dr. J. C. ARTHUR—and this is translated into German. The only English pages are those of Dr. D. H. SCOTT on "The fern-like seed-plants of the carboniferous flora." A good index makes available the entire contents. The two volumes should be in every botanical reference library.—C. R. B.

Knuth's Handbook.

In 1899 the first volume of KNUTH's *Handbuch der Blütenbiologie* appeared,[3] based on HERMANN MULLER's *Die Befruchtung der Blumen durch Insekten*. It is general and deals with the structure of flowers and of insects in relation to pollination. In the same year the second volume appeared,[4] giving an account of all known observations upon the pollination of the flowers of arctic and temperate zones. The third and last volume was published after the death of KNUTH, under the editorship of LOEW, and deals similarly with plants from countries other than Europe. The Clarendon Press has undertaken the publication of an English translation, the first volume of which has lately appeared,[5] and the second volume is announced as being in press. The translator is J. R. AINSWORTH DAVIS, Trinity College, Cambridge, and the prefatory note is by Professor I. B. BALFOUR.

The character of this encyclopedic work is well known to students of pollination, and it is a great boon to English and American botanists to possess it in an English translation. The original text appeared in instalments, and the appendices of supplementary information have been incorporated in the body of the text by the translator. A special feature of the translation is the bringing together in one list all the citations in the original, and completing the record to January 1, 1904. The number of citations is almost beyond belief, the botanical titles in the bibliographical list reaching 3748. It must be said, however, that the citations are probably more numerous than significant, as a cursory examination suggests. There are frequent cases where "fertilization" is confused with "pollination," and papers cited which can hardly be imagined as belonging to the real literature of pollination. Then too, there is occasional duplication of titles, as for example titles 633 and 643, which are identical in every particular. The dreadful task of editing such a mass of citations should

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[3] BOT. GAZETTE **28**:280. 1899.

[4] BOT. GAZETTE **28**:432. 1899.

[5] KNUTH, PAUL, Handbook of flower pollination. Translated by J. R. AINSWORTH DAVIS. Volume I. 8 vo. pp. xix+382. Oxford: Clarendon Press. 1906.

excuse many slips, but the serious question is as to the value of such a mass of undigested citations.

In any event, the translation is exceedingly welcome, and should go far toward stimulating a study to which American botanists pay scant attention. —J. M. C.

A New Zealand Manual.

IN 1864 Sir JOSEPH D. HOOKER published the first part of his *Handbook of the New Zealand Flora*, which belonged to a uniform series of floras contemplated for all the British colonies. In 1894 the late Mr. T. KIRK was engaged by the New Zealand government to prepare a *Student's Flora* of New Zealand, but at his death in 1897 barely two-fifths of this task had been completed. This fragment has since been published by the government, but the need for a complete and convenient flora was becoming so acute that in 1900 Mr. T. F. CHEESEMAN, curator of the Auckland museum, was appointed by the government to prepare a *Manual of the New Zealand Flora*, and this has now appeared.[6]

The instructions to the author included one to follow the general plan of HOOKER'S *Handbook*, and another to include only indigenous plants. However, in an appendix the New Zealand families are arranged in the Engler and Prantl sequence; a list of the naturalized plants is also given, and a very long one it is. There is also an alphabetical list of Maori names of plants, and a full glossary. A most interesting and valuable contribution, contained among the introductory pages, is "A history of botanical discovery in New Zealand," from Cook's first visit in 1769 to the present year.

As is customary, only the vascular plants are included, and the range covered includes not only the two main islands of the Colony of New Zealand, but also the outlying groups of the Kermadec Islands, the Chatham Islands, the Auckland and Campbell Islands, Antipodes Island, etc. Macquarie Island is also included, although it belongs to Tasmania, because it is more closely allied in its flora to the Auckland and Campbell Islands than to any other land. The descriptions are in almost all cases original, and have been based upon the examination of living or dried material, extending through thirty-five years of continuous study and collection of the flora. Surely no one of larger experience could have been selected to do this work, which gives evidence throughout of most painstaking care and most orderly and clear presentation.

The composition of this flora makes it one of the most interesting on the globe, and hence a few general data concerning it will not be out of place. The volume includes the descriptions of 1571 species, only 156 of them being pteridophytes. The four largest families, with species numbering from 221 down to 113, are Compositae, Cyperaceae, Scrophulariaceae, and Gramineae; and the Compositae constitute one-seventh of the whole flora. The largest genus is Veronica,

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[6] CHEESEMAN, T. F., Manual of the New Zealand Flora. 8vo. pp. xxxvi+1199. Wellington: Published under the authority of the Government of New Zealand. 1906.

with 84 species, followed by Carex, Celmisia (Compositae), Coprosma (Rubiaceae), Ranunculus, Olearia (Compositae), etc. Numerous new species are described and a new genus (*Townsonia*) of Orchidaceae is established. The most remarkable fact is that of the 1571 species 1143 are endemic, nearly three-fourths of the entire flora. Of the 428 species found elsewhere, 366 extend to Australia, and 108 to South America. This almost complete "strangeness" of the flora to botanists who are familiar with the north temperate floras and who have even visited the tropics, gives it a fascination suggestive of just as strange results if such material could be made available in their laboratories. – J. M. C.

MINOR NOTICES.

Development of fern leaves.—MARGARET SLOSSON has brought together in an elaborate book a remarkable series of observations upon the development of fern leaves.[7] She has selected nineteen representative species from northeastern United States, and illustrated them by forty-six handsome plates reproduced from photographs. A preliminary chapter contains a general description of the development of form and venation, often showing remarkable changes in passing from the juvenile to the mature form. In the subsequent chapters each species is first described in its mature form, and then follows a very detailed description of the transition forms from the juvenile stage. The possible range of leaf variation is also considered. The book contains a mass of suggestive observations, which should serve as a check to any characterization of species from insufficient material, and as a demonstration that the numerous "form species" of fossil "ferns" are more than doubtful. The book is more of a contribution than its elaborate form would suggest.—J. M. C.

Portraits of botanists.—DÖRFLER, editor of *Botaniker-Adressbuch*, has issued the first two parts of a proposed series of portraits of botanists. Each part contains ten portraits, $9 \times 12.5^{\mathrm{cm}}$, which are phototype reproductions upon fine art cards, each card also bearing the signature of the botanist in facsimile. The cards are loose, being ready to frame and worthy of it. It is announced that 100 portraits, with title page and index, will form a volume. A grape of text accompanies each portrait, giving the most important biographical data and bibliography. Each part costs 5 marks to subscribers; single portraits can be obtained for 1 mark; and 10 selected portraits for 8 marks. The first part contains portraits of KERNER, WIESNER. WARMING, ENGLER, DEVRIES, GUIGNARD, SCHRÖTER, MATTIROLO, WILLE, and WETTSTEIN; the second part, FRIES, (Elias and Theodor), PFEFFER, BORODIN, HACKEL, SCOTT, GOEBEL, ERRERA, CHODAT, and IKENO. The address is J. DÖRFLER, Barichgasse 36, Wien, III.—J. M. C.

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[7] SLOSSON, MARGARET, How ferns grow. 8vo. viii+156. New York: Henry Holt & Company. 1906.

Ustilaginales of the North American Flora.—Another part of the *North American Flora* has appeared, containing the Ustilaginales by CLINTON.[8] The changes from a former monograph[9] by the same author are mostly such as adapt the monograph to the style of the *Flora*. The older European synonomy, the list of species showing general distribution, and the extensive bibliography of the former publication are omitted. The omission of the general notes relating to the genera and species is a distinct disadvantage. It takes away from the descriptions all that individuality which helps the mind to recognize a plant from its description far more readily than do the technical diagnoses. The host index in its present alphabetical arrangement of hosts, with page references to the parasites, represents a marked improvement over the former arrangement. Artificial keys for the determination of species have been added under the genera. —H. HASSELBRING.

Index Filicum.—This work is completed by the twelfth fascicle[10], which concludes the catalogue of literature, and also includes a systematic enumeration of the genera. It appears that 23,499 names are cited, but that only 149 generic names and 5940 specific names stand. It is interesting to note that these species are distributed among the 12 families as follows: Hymenophyllaceae 462, Cyatheaceae 456, Polypodiaceae 4527, Parkeriaceae 1, Matoniaceae 2, Gleicheniaceae 80, Schizaeaceae 118, Osmundaceae 17, Salviniaceae 18, Marsileaceae 63, Marattiaceae 118, Ophioglossaceae 78. This sequence of families is that used by the author. The parts have appeared with most commendable promptness, and the completed volume will be a most useful one.—J. M. C.

Trees of the Amazon region.—HUBER has issued the third and fourth decades of his *Arboretum Amazonicum*,[11] the first two parts having appeared in 1900.[12] The superb quality of the plates is maintained, and, as before, each plate is accompanied by at least a page of descriptive text in Spanish and French in parallel columns. There are habit studies of different palms, legumes, etc., views of different types of savannas, characteristic river-bank vegetation, forest interiors, effect of wind on trees, etc. These glimpses of tropical plants and plant formations are among the very finest that have been published.—J. M. C.

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[8] CLINTON, G. P., Ustilaginales. North American Flora **7**: part 1. pp. 82. October 4, 1906.

[9] North American Ustilaginaeae. Proc. Boston Soc. Nat. Hist. **31**:329–529. 1904. Reviewed in BOT. GAZETTE **39**:314. 1905.

[10] CHRISTENSEN, C., Index Filicum, etc., Fasc. 12. Copenhagen.: H. Hagerup. 1906. *3s. 6d.*

[11] HUBER, J., Arboretum Amazonicum. Iconographie desplantes spontanées et cultivées les plus importantes de la région Amazonienne. Decades 3 and 4. 4to. Para. 1906. Each decade 10 fr.

[12] BOT. GAZETTE **33**:72. 1902.

Ptelea.—A revision of this genus as it occurs in western and southwestern United States and Mexico has been published by GREENE.[13] Under his treatment the genus has become rich in species, 59 being recognized, of which 55 are new. Three natural groups are defined, each with its own geographical range: (1) species (37) with chestnut-brown twigs and prevailingly glaucescent or bluish-green foliage; (2) species (13) with amost white twigs and yellow green foliage; (3) species (9) with cinnamon-colored twigs, a peculiar hue and venation of foliage, and narrow-winged or even wingless samaras.—J. M. C.

Anatomy of Commelinaceae.—HOLM has published an elaborate memoir[14] dealing chiefly with the general morphology and anatomy of the Commelinaceae. The 17 species investigated represent the genera Commelina (5), Aneilema, Tinantia, Tradescantia (9), and Weldenia. The memoir is a mine of information which can be drawn upon by the future student of the group who is seeking to organize such details into general statements.—J. M. C.

Genera Siphonogamarum.—The eighth fascicle of DALLA TORRE and HARMS'S[15] list of the genera of seed plants concludes the genera of Compositae, 9629, Thamnoseris being the last one. The genera of uncertain affinity swell the number of genera to 9810. There is also a supplement of 51 pages, and the general index of names is begun.—J. M. C.

NOTES FOR STUDENTS.

Ancient Araucarians.—In Jurassic and Cretaceous deposits there occur abundant remains of leafy branches of coniferous plants that have been described under the generic name Brachyphyllum. The genus has been referred by various authors to Araucarineae, to Cupressineae, and to Taxodineae (near Sequoia); but in a recent paper by JEFFREY and HOLLICK[16] it is shown from an investigation of the internal structure that here can be no doubt as to its Araucarian affinities. In the same paper *Protodammara* is described as a new genus, to include certain Cretaceous cone scales that had been referred to the living genus Agathis (Dammara). Certain lignites associated with both Brachyphyllum and Protodammara were also found to be Araucarian; and the conclusion is reached that these lignites represent the wood of the trees which bore the leafy

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[13] GREENE, EDWARD L., The genus Ptelea in the western and southwestern United Stated and Mexico. Contrib. U. S. Nat. Herb. **10**:49–79. 1906.

[14] HOLM, THEODORE, Commelinaceae. Morphological and anatomical studies of the vegetative organs of some North and Central American species. Memoirs Nat. Acad Sci. **10**:159–192. *pls. 1–8.* 1906.

[15] DALLA TORRE, C. G. DE and HARMS, H., Genera Siphonogamarum ad systema Englerianum conscripta. Fasc. 8. pp. 561–640. Leipzig: Wilhelm Engelmann. 1906. *M6.*

[16] HOLLICK, A., and JEFFREY, E. C., Affinities of certain Cretaceous plant remains commonly referred to the genera Dammara and Brachyphyllum. Amer. Nat. **40**: 189–215. *pls. 1–5.* 1906.

branches called Brachyphyllum and the cones called Protodammara. This multinomial genus was thought by the authors to be "in all probability the last survivor of an ancient Araucarian line of descent, joined near its base with the primitive stocks of the Abietineous and Cupressineous series."

More recently JEFFREY has been able to study the wound reactions of Brachyphyllum and to draw from them more definite conclusions as to its relationships.[17] In a well-preserved specimen of the wood, Brachyphyllum can be distinguished at once from any living Araucarian by the absence of resiniferous elements other than those found in the pith-rays. In this feature the genus resembles such old gymnosperm groups as the Pteridospermae, Cordaitales, and Cycadales, and also the very ancient but still flourishing genus Pinus. JEFFREY further finds that Brachyphyllum agrees with the Abietineae in its traumatic reactions, resin-canals being formed as a result of wounding. Following the line of reasoning used in connection with his work on Sequoia,[18] he concludes that these reactions furnish one evidence that the Araucarieae are phylogenetically connected with the Abietineae; and that Agathis and Araucaria hold the same relation to Brachyphyllum that the other genera of the Cupressineae hold to Sequoia. This phylogenetic linking together of both the Cupressineae and Araucariaeae with the very ancient Abietineae is especially interesting on account of the very isolated position of existing Araucarians among existing Coniferales, and also on account of SEWARD's recently expressed views[19] in reference to the relationships and origin of the Araucarians.—J. M. C.

Adsorption of chlorophyll.—It has always been troublesome to explain the differential extraction of the chlorophyll pigments by their solvents under various conditions, and TSWETT seeks to supply a better theory.[20] Thus, fresh leaves or those ground in a mortar with sand or emery and covered with petrolether yield a more or less pure-yellow extract of carotin, with traces of other pigments. Dried leaves, even at a lower temperature, yield even purer carotin. But boiled leaves, or even warmed tissues, yield green extract. Alcohols (methyl, ethyl, and amyl), acetone, acetaldehyde, ether, and chloroform give a green extract with fresh, dry, or boiled leaves, dissolving all pigments freely. It suffices to add a little alcohol (10 per cent. for fresh, 1 per cent. for dry leaves) or the other solvents to petrolether to secure a beautiful green extract. How explain these facts?

If strips of filter paper be put into a flask with an alcohol-petrolether solution and the solvent evaporated *in vacuo*, the pigments become concentrated in the paper. This dry green paper now behaves toward solvents exactly as above stated for the green leaves. This, TSWETT holds, indicates that the pigments[21]

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[17] JEFFREY, E. C., The wound reactions of Brachyphyllum. Annals of Botany **20**:383–394. *pls. 27–28.* 1906.

[18] See BOT. GAZETTE **38**:321. 1904.

[19] See BOT. GAZETTE **42**:224. 1906.

[20] TSWETT, M., Physikalisch-chemische Studien über das Chlorophyll. Die Adsorptionen. Ber. Deutsch. Bot. Gesells. **24**:316–23. 1906.

are absorbed by the stroma, i. e., held mechanically by molecular affinity, and in different degrees under different conditions, this molecular attraction being overcome by the various solvents unequally. Consequently, it is argued, the pigments cannot exist as grana in the stroma—a conclusion already indicated by recent study both with microscope and ultramicroscope. Many bodies beside cellulose hold the pigments in like fashion. The work is suggestive, but TSWETT'S crucial experiment is not convincing.

Inasmuch as the different pigments are held fast unequally, if a petrolether solution, or even better a solution in carbon bisulfid, be filtered through a column of calcium carbonate, the pigments are distributed in zones, the more firmly adsorbed ones above, the less firmly fixed successively lower. Such a preparation he calls a chromatogram, and the method the chromatographic method.[21]

In a later paper[22] TSWETT gives further details of the technique and analyzes the zones of his chromatogram. The synonymy of the chlorophyll pigments is so tangled that it is almost impossible to compare the work of different investigators. The chromatographic method promises to be of use in demonstrating that there are different pigments, but its value in research seems questionable. —C. R. B.

The Svalöf Experiment Station.—Although the work of the Swedish Agricultural Experiment Station at Svalöf is widely celebrated because of its noteworthy economic results, these results and the means by which they have been attained are not generally understood, owing to the fact that all of its reports are printed in the Swedish language. DE VRIES has devoted two recent papers[23] to a discussion of the Svalöf methods and their scientific significance. In the first of these papers is given a brief history of the station, together with an exposition of the methods employed. The history of the station falls rather naturally into four 5-year periods, each marked by a characteristic advance. During the first period, 1886–1891, the work of introduction and testing of varieties, in the way usually done by Agricultural Experiment Stations, presents nothing unique, the several sorts being treated as units. With the appointment of Dr. H. NILSSON as Director in 1890 begins the second period, in which the discovery was made that each variety is a mixture of a large number of elementary forms and that the latter are the real units with which scientific agriculture must deal. In the third period was carried out the great work of segregating the elementary

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[21] TSWETT proposes to call the collective green pigment of leaves chlorophyll; the green fluorescent components chlorophyllins; the yellows already are distinguished as carotins and xanthophylls.

[22] TSWETT, M., Adsorptionsanalyse und chromatographische Methode. Anwendung auf die Chemie des Chlorophylls. Ber. Deutsch. Bot. Gesells. **24**:384–393. 1906.

[23] DEVRIES, HUGO, Die Svalöfer Methode zur Veredelung landwirthschaftlicher Kulturgewächse und ihre Bedeutung für die Selektionstheorie. Arch. für Rass. u. Gesells.-Biol. **3**:325–358. My-Je 1906.

Altere und neuere Selektionsmethode. Biol. Centralbl. **26**:385–395. Jy 1906.

forms, studying their morphological characters, and testing their relative value by parallel cultures. During the last five years the successive generations of these segregated pure races have been followed, with the result that a considerable number of mutants have been found and tested. In both papers DEVRIES compares NILSSON'S pedigree-culture method with the older and still almost universal method of selection in which the undesirable individuals are destroyed and all the best are saved and sown together. He concludes that RIMPAU could have produced the Schlanstedt barley, for which he is so widely celebrated, in four or five years by the Svalöf method, instead of having to devote to it the 20–25 years required by the older method. The magnitude and quickness of the results at Svalöf, where alone the conception of constant elementary forms has been adopted as the basic principle, indicates the importance of the newer conceptions of evolution for scientific agriculture, and these papers of DEVRIES bring to the notice of the non-Swedish world methods which will doubtless lead to most important changes in the conduct of the various agricultural stations.—GEO. H. SHULL.

Report to Evolution Committee.—In a third report to the Evolution Committee of the Royal Society, BATESON, SAUNDERS, and PUNNETT[24] have shown that practically all the complexities encountered in their study of hybrid stocks, sweet peas, and poultry are in essential accord with Mendelian expectation if the assumption is made that what appears externally as a single character may be in reality dependent for its appearance upon the presence of two or more independent allelomorphs or internal units. In some cases the nature of these internal units is apparent, as when the presence of one always changes a pigment from red to blue; but in other cases there is no clue to the nature of the individual allelomorph, as when the combination of two white sweet peas invariably produce colored offspring owing to the bringing together of two allelomorphs the combined action of which is necessary to the production of color. In stocks the presence of hoary pubescence is shown to depend upon the simultaneous presence of four independent allelomorphs, two of which are also necessary to the production of colored flowers. At the New Orleans meeting of the Botanical Society of America (December 1905) the reviewer presented a paper on the "Latent characters of a white bean," in which it was shown that the color of purple mottled beans obtained as an F_1 from a cross between yellow and white is dependent upon the simultaneous presence of three distinct allelomorphs. In that paper it was predicted that BATESON'S results on stocks and sweet peas would find a satisfactory explanation on the same grounds without the assumption of complex and inexplicable synthesis and resolution of "hypallelomorphs" as attempted in the earlier Reports to the Evolution Committee. The completeness with which the new point of view is demonstrated by these further investigations will do much to strengthen the view that Mendelian behavior is a more common

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[24] BATESON, W., SAUNDERS, Miss E. R., PUNNETT, R. C., Reports to the Evolution Committee. III., pp. 52. London: Harrison & Sons. 1906.

phenomenon than previous observations would have indicated. Although stocks behave in a rather simple way when the analysis given by the authors is comprehended, the recombination of the allelomorphs that have been discovered in this plant yields in the second generation 243 distinct types, and it is plain that in still more complex cases a perfectly typical Mendelian behavior would easily exceed the keenest human power of analysis to unravel. —GEO. H. SHULL.

Sterilized soil.—SCHULZE finds[25] that plants grown in sterilized soil are affected by two opposing factors· (1) the formation of more or less injurious decomposition products in the sterilizing process, which act upon the plants "according to the degree of their sensitiveness" (this phrase obviously hides ignorance of other factors); (2) an advantageous release of nutritive materials, especially of the otherwise unavailable nitrogen. According as one or the other of these factors prevails the crop is increased or diminished by sterilizing the soil. But even when the crop is diminished the N-content may be markedly increased. By the addition of lime the injurious effect of the decomposition products may be almost or wholly counteracted. The significance of these researches for pot-cultures in sterilized soil is obvious, invalidating many conclusions based upon such experiments when this factor had not been considered.—C. R. B.

Moss rhizoids.—KURT SCHOENE finds[26] that rhizoids rarely arise from the germinating spores of any mosses except Funaria, in which they regularly appear. Lack of nitrogen suppresses the chloronema of Funaria, reducing it much in others; and lack of either nitrates or phosphates enormously lengthens the rhizoids of Funaria. These peculiarities of spore germination mark Funaria as a ruderal plant. The rhizoids show a gradation in their significance as organs of food supply, diminishing from the forms with a central strand to those without it, this function entirely disappearing in water forms. (The experiments on which this statement rests are too few and inconclusive to be convincing.) The oblique position of partitions is held to be a mechanical arrangment for resisting longitudinal strains and too great deformation of plasma on bending. It is not obvious that in nature such dangers often threaten.—C. R. B.

Items of taxonomic interest.—OAKES AMES (Proc. Biol. Soc. Washington **19**:143–154. 1906) has described 18 new species of Acoridium (Orchidaceae) from the Philippines.—R. SCHLECHTER (Bull. Herb. Boiss. II. **6**:843. 1906), in Loesener's *Plantae Selerianae*, has described a new genus (*Labidostelma*) of Asclepiadaceae from Guatemala.—C. B. CLARKE (Kew Bull. 1906:251) has published a new African genus (*Crossandrella*) of Acanthaceae.—A. D. E. ELMER (Leaflets on Philipp. Bot. **1**:42–73. 1906) has published new Philippine species under Pandanus (2), Ficus (8), and the Rubiaceae (14).—J. M. C.

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[25] SCHULZE, C., Einige Beobachtungen über die Einwirkung der Bodensterilisation auf die Entwickelung der Pflanzen. Landw. Versuchs-Stat. **65**:137–147. 1906.

[26] SCHOENE, KURT, Beiträge zur Kenntnis der Keimung der Laubmoossporen und zur Biologie der Laubmoosrhizoiden. Flora **96**:276–321. 1906.

NEWS.

Chester A. Darling, Albion College (Mich.), has been appointed assistant in botany at Columbia University.

Dr. Albert Mann, Department of Agriculture, has been appointed professor of botany at George Washington University.

A biographical sketch, with portrait, of the late C. B. Clarke is published in *Journal of Botany* for November, having been prepared by D. Prain and W. H. Bliss.

Professor L. H. Bailey, Cornell University, was elected president of the Association of Agricultural Experiment Stations at the recent Baton Rouge meeting.

Mr. A. C. Seward, formerly university lecturer, has been elected to the professorship of botany at Cambridge made vacant by the death of Professor H. Marshall Ward.

Professor Roland Thaxter, Harvard University, has returned from his year's leave of absence. A portion of his time was spent in South America and included a collecting trip to the Straits of Magellan.

The date of publication of the November Gazette should have been given as November 30 instead of November 17. After the number was printed publication was delayed by unforseen difficulties with the plates, due to a lithographer's strike.

In connection with the recent quatercentenary celebrations of the University of Aberdeen, honorary degrees were conferred on the following botanists: Casimir DeCandolle, Geneva; Hugo DeVries, Amsterdam; J. Matsumura, Tokyo; and D. H. Scott, Kew.

It is appropriate to call attention again to the limitations which the Editors have been obliged to establish for papers published in the Gazette. No article exceeding thirty-two pages is acceptable, except with the consent of the author to pay for the pages in excess of thirty-two, which will be added to the usual number.

The Department of Agriculture, in its Yearbook for 1905, publishes a paper on the progress of forestry during that year. The year is regarded as "an epoch in the history of American forestry," chiefly because during that year it "passed out of the stage of preparation and propaganda into that of actual work." On February 1, 1905, the administration of the national forest reserves came under the Department of Agriculture, and by the end of that year an efficient system of forest administration was being inaugurated upon a hundred million acres of forest lands.

THE ROYAL SOCIETY of London has awarded recently the following medals to botanists: A Royal medal to Dr. D. H. SCOTT for his investigations and discoveries in connection with the structure and relationship of fossil plants; the Darwin medal to Professor HUGO DEVRIES on account of the significance and extent of his experimental investigation in heredity and variation.

THE FIRST SESSION of the next annual meeting of the American Association will be held at Columbia University on the morning of Thursday, December 27. During Thursday and Friday Section G will meet at Columbia University; but on Saturday it will meet in connection with the Botanical Society of America at the New York Botanical Garden. The meetings will continue on Monday and Tuesday, or as long as is required by the program.

THE UNIVERSITY OF CALIFORNIA has received by donation the herbarium and botanical library of Mr. and Mrs. T. S. BRANDEGEE, of San Diego. The herbarium is one of the most important in the west, since it contains something over 100,000 sheets of carefully selected plants, mostly representative of the Mexican flora, which for many years has been Mr. BRANDEGEE'S chosen field, and of the flora of California and neighboring states, which has received careful treatment at the hands of Mrs. BRANDEGEE. It contains the sole remaining duplicate types of many species, the originals of which were lost in the recent fire that destroyed so large a portion of the herbarium of the California Academy of Sciences as well as the types of practically all the new species described by Mr. and Mrs. BRANDEGEE themselves. Among the noteworthy sets represented are BEBB'S willows, PARRY'S Manzanitas and Chorizanthes, a majority of the Mexican sets distributed by PALMER, PRINGLE, LUMHOLTZ, PURPUS, etc., and a selection of types and duplicate types from the ORCUTT and CLEVELAND herbaria. It is probable that no other herbarium contains so nearly complete a representation of the North American Borraginaceae. It is also rich in Mimulus, Eriogonum, and other groups in which Mrs. BRANDEGEE has been particularly interested.

The University Herbarium, as now enlarged, numbers approximately 250,000 sheets, a majority of which are mounted in permanent form. The whole collection is available for study and occupies fire-proof quarters in one of the buildings recently erected on the University campus. Here visiting botanists desiring to study the West American and Mexican flora or to consult the working library of the herbarium, will be welcome and given every opportunity for research work, Mr. and Mrs. BRANDEGEE will continue their studies at the University where Mr. BRANDAGEE has been appointed Honorary Curator of the Herbarium. Mail matter may hereafter be addressed to them at the University.

GENERAL INDEX.

The most important classified entries will be found under Contributors, Personals, and Reviews. New names and names of new genera, species, and varieties are printed in **bold-face** type; synonyms in *italic*.